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A Morphological Study of Stylidium graminifolium

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INTRODUCTION

The Australasian family Stylidiaceae differs markedly, in certain structural features, from other families of angiosperms. The androecium is represented by two stamens which are completely fused with the style to form a column or gynostemium. The result is that the anthers are apparently sessile, one lying on each side just below the stigma. The family is also very peculiar because it shows a discontinuous and disproportionate distribution (Good, 1925 and 1947) over two widely isolated land areas. It includes six genera (Engler, 1908) and 129 species. Starting from Australia, members of this family extend to the eastern portion of India and Ceylon via Burma along one direction, and along the other to South America through New Zealand across the South Pacific. *Stylidium* is the largest genus with no less than 112 species. Three of these are found in the Indian subcontinent. These are *Stylidium tenellum*, *S. kunthii* (Burma and East Bengal) and *S. uliginosum* (Ceylon).

PREVIOUS LITERATURE

The earliest work on the morphology and embryology of *Stylidium* is that of Burns (1900). He has described in detail the anatomy of the leaf and stem in several species adding at the same time a note on the structure of epidermis, stomata, glands and hairs. He reported that in *S. squamellosum* the female gametophyte is of the Polygonum type. The endosperm is said to be free nuclear in the beginning but later becomes cellular and develops haustoria at the micropylar and chalazal ends. Burns also states that immediately after the entrance of the pollen tube, the micropylar part of the embryo sac grows into an enormous haustorium much larger than the rest of the sac and there is a conspicuous integumentary tapetum investing the lower part of the embryo sac which has a gland-like nutritive tissue at its chalazal end.

The latest contribution on the embryology of this family is that of Rosén (1935) on *S. adnatum*. He has shown that the ovary, though bicarpellary, is usually unilocular, for the other locule is represented in an atrophied state. The embryo sac is of the Polygonum type with elongated synergids. The endosperm is cellular and resembles the Scutellaria type (Schnarf, 1931), the micropylar endosperm haustorium being more aggressive than the chalazal.

MATERIALS AND METHODS

Material of *Stylidium graminifolium* Swartz. was collected in formalin-acetic-alcohol by Mr. O. D. Evans from Liverpool, New South Wales, Australia. The plants were growing on sandy soil in an open forest. The material was dehydrated and embedded in paraffin in the usual manner and sections were cut at a thickness of 10 to 20 microns. Since the inner layers of the fruit wall become sclerosed, great difficulty was experienced in cutting the mature fruits. This was overcome by removing the seeds from the fruit before embedding them in paraffin. The sections were stained in Heidenhain's iron alum Haematoxylin with eosin as a counter stain.

ORGANOGENY

The axis of the inflorescence is circular in transverse section (Fig. 9) and the florets are arranged spirally in the clockwise direction. Sections through the young inflorescence show that the bract is a lateral outgrowth (Fig. 1) in whose axil arises the floral primordium (Fig. 2). This soon differentiates into the floral receptacle and the pedicel (Fig. 3). On the receptacle the calyx, corolla, stamens and carpels arise in acropetal succession (Figs. 4–7). In an older bud (Figs. 8, 31) the calyx is made up of two lobes, the anterior one of which encloses the posterior. The corolla comprises five imbricately arranged petals, the anterior one of which, called the labellum, is small and usually has two lateral linear appendages (Fig. 29). Of the remaining petals, the postero-lateral ones bear two appendages each and the antero-laterals bear a single appendage each (Fig. 29). Each appendage bears a number of papillose cells at its apex (Fig. 30).

Figs. 9 to 26 represent a series of transverse sections of a young flower bud, passing from the base to the top to show the origin of the floral parts. The bract (Figs. 10–12) lies on the anterior side and the two bracteoles lie laterally (Figs. 13–15). Next are the two carpels of the inferior ovary. The anterior one, which is slightly larger, always precedes and develops first (Figs. 15–17). The anterior lobe of the calyx also differentiates first and encloses the posterior one (Figs. 17–21). Of the petals, the labellum (Figs. 18–20) which differs in shape from the remaining petals differentiates first (Fig. 29). The antero-lateral (Figs. 22, 23) and postero-lateral petals arise successively (Figs. 24, 25) from a common primordium of the corolla (Fig. 22). They show an imbricate arrangement (Fig. 29), only the labellum being free. The arrangement of the floral parts is shown in the floral diagram (Fig. 31).

THE COLUMN

The flower is peculiar in having a column. The latter originates from the apex of the inferior ovary and represents the fused style and

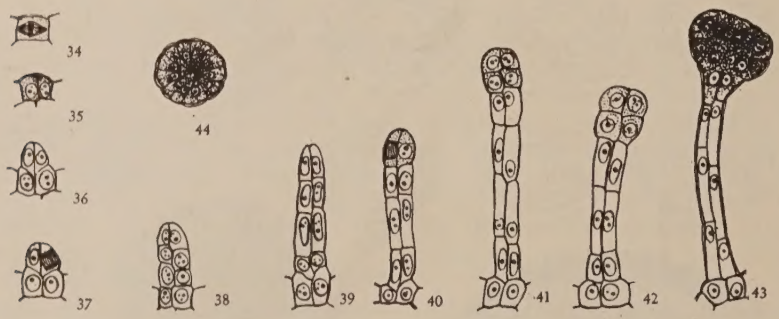
stamens. The postero-lateral stamens are completely fused with the style. The column is broadly oval in transverse section (Fig. 27) with two prominent vascular bundles on either side which form the supply

FIGS. 1–8. L. S. young flower buds to show the origin of the floral parts. × 26. FIGS. 9–26. T. S. of young flower bud from the base upwards, showing the origin of the floral parts. × 26. FIG. 27. T. S. of the column. × 87. FIG. 28. Bilobed stigma with the papillose cells. × 112. FIG. 29. Aestivation of the corolla and its appendages. × 13. FIG. 30. Enlarged view of one of the petal appendages. × 43. FIG. 31. Floral diagram. FIG. 32. T. S. flower at the base of column to show the two nectaries. × 60. FIG. 33. L. S. nectary; note the well-developed vascular supply. × 43.

to the two stamens. The epidermal cells of the column are radially elongated and densely protoplasmic. The central portion of the column is made up of small compactly arranged cells with granular cytoplasm, while the cells lying on the sides are larger and more loosely arranged. The apex of the column ends in a bilobed stigma (Fig. 28) and lateral to it are the two subconfluent sessile anthers. The epidermal cells of the stigma are papillate and densely cytoplasmic. Those situated on the inner surface of the stigmatic lobes become interlocked (Fig. 28). Barnes (1885) records a similar condition in *Campanula patula* and considers it to be a device for preventing the premature separation of the lobes.

NECTARY

Two conspicuous nectaries, the anterior one of which is larger, are present at the base of the column and immediately above the inferior ovary (Fig. 32). Each nectary consists of glandular cells with conspicuous nuclei and dense contents and is strongly vascularised (Fig. 33). Such nectaries are also present in members of the Lobeliaceae (Subramanyam, 1949) and Goodeniaceae (Brough, 1925).



FIGS. 34–44. Stages in the development of the multicellular glands. × 129.

GLANDS

Numerous stalked multicellular glands are present on the axis of the inflorescence, bract, bracteoles, sepals, petals and the outer wall of the inferior ovary. Such glands also occur in other species of *Stylidium* (Burns, 1900). An epidermal cell first undergoes an anticlinal division (Fig. 34) resulting in two cells which slightly protrude above the general surface of the epidermis (Fig. 35). Both of these cells divide transversely (Fig. 36). The inner two cells merge with the remaining cells of the epidermis (Fig. 37) while the outer undergo further transverse divisions to produce a biseriate filament of four to five cells (Figs. 37 to 39). Of these the lower cells form the biseriate stalk and only the two topmost cells take part in the formation of the gland. They enlarge and usually undergo a transverse (Fig. 40) or rarely a vertical division. The four cells (Fig. 41) thus formed divide in a plane at right angles to the first resulting in eight cells arranged in two tiers of four cells each (Fig. 42). The cells of both these tiers produce the multi-

cellular gland by further anticlinal divisions (Fig. 43). In surface view (Fig. 44) the gland appears circular consisting of radially arranged cells.

THE MICROSPORANGIUM AND MALE GAMETOPHYTE

A transverse section of the young anther lobe shows a plate of four to six hypodermal archesporial cells (Fig. 45) which divide periclinally to form the primary parietal and primary sporogenous cells (Fig. 46). The primary parietal layer undergoes further periclinal divisions to form the anther wall and, after undergoing a few more divisions, the sporogenous cells are converted into spore mother cells (Fig. 47). The outermost layer in the anther is the epidermis, next comes the endothecium, then a middle layer which soon becomes flattened and crushed, and finally the glandular tapetum whose cells are uninucleate

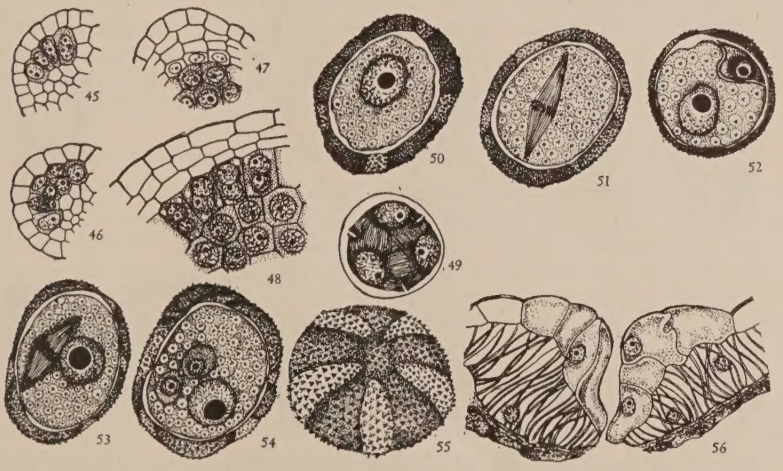


FIG. 45. Portion of cross section of an anther showing archesporial cells. × 253. FIG. 46. Formation of the primary parietal and primary sporogenous layers. × 253. FIG. 47. Portion of young anther showing epidermis, endothecium, middle layer, uninucleate tapetum, and sporogenous cells. × 253. FIG. 48. Same at a later stage showing binucleate tapetum. × 253. FIG. 49. Quadripartition of microspores by the formation of cleavage furrows. × 843. FIG. 50. Uninucleate microspore. × 590. FIG. 51. First division of microspore. × 590. FIG. 52. Two-celled pollen grain showing the large vegetative cell and lenticular generative cell. × 590. FIG. 53. Division of generative nucleus. × 590. FIG. 54. Mature pollen grain showing the tube nucleus and the male cells. × 590. FIG. 55. Surface view of pollen grain, showing the five conspicuous bands. × 590. FIG. 56. Portion of mature anther to show the stomium, fibrous endothecium, and disorganizing middle layer and tapetum. × 253.

at first (Fig. 47) but later become binucleate (Fig. 48) as in the Campanulaceae (Kausik and Subramanyam, 1946b, 1947b, Subramanyam, 1948) and Lobeliaceae (Kausik, 1938, Hewitt, 1939, Cooper, 1942, Kausik and Subramanyam, 1945a and b and Subramanyam, 1950). The microspore mother cells undergo the usual reduction divisions and form tetrads of microspores. Quadripartition of the microspore mother cells takes

place by peripheral cleavage furrows (Fig. 49) and the microspores are arranged tetrahedrally.

In the mature anther (Fig. 56) the tapetum and the middle layer are disorganised and the endothecium develops the usual fibrous thickenings. At the line of dehiscence some of the epidermal cells enlarge conspicuously and constitute the stomium.

As a result of the first division of the microspore (Figs. 50, 51) a small lenticular generative cell (Fig. 52) is cut off from a larger tube cell. The former divides (Fig. 53) to produce the two male cells (Fig. 54). This is the shedding stage of the pollen. Starch grains are abundant in all stages of development of the pollen grain (Figs. 50–54). They have also been shown to occur in the mature pollen grains of *Cephalostigma Schimperi* (Kausik and Subramanyam, 1947a), a member of the Campanulaceae. The mature pollen grain is oval in outline and

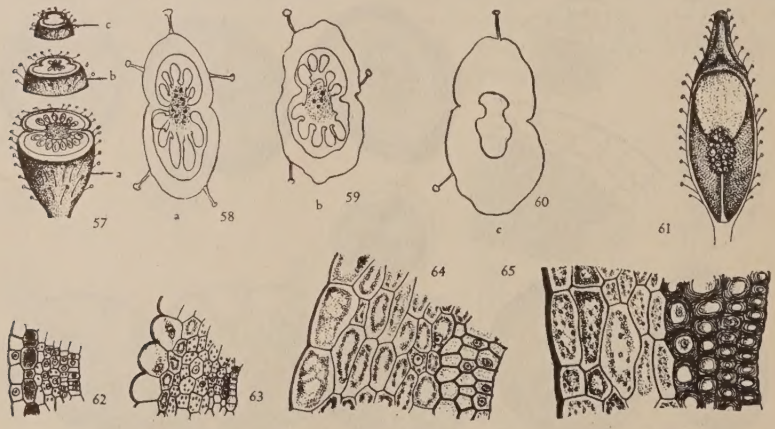


FIG. 57. A three dimensional view of sections of ovary at different levels. × 3. FIGS. 58–60. T. S. of the ovary at levels a, b and c, marked above. × 26. FIG. 61. L. S. ovary parallel to the septum to show its unilocular nature at the top. × 3. FIGS. 62–65. Portions of ovary wall at various stages in the development of the fruit; note that in later stages the inner layers of the wall get strongly sclerosed. × 112 each.

has six prominent bands going around it (Fig. 55). The exine is fairly thick and is closely and minutely echinulate. The germ pores are indistinct at first, but become quite conspicuous at the time of germination and are slit-like in appearance.

In some anthers the pollen grains had germinated *in situ*. Since the pollen tube was filled with densely staining material it was difficult to make out the tube nucleus and the male cells. A similar precocious germination of the pollen grains has been recorded in *Lobelia trialata* (Kausik and Subramanyam, 1945b) and *L. pyramidalis* (Subramanyam, 1949).

STRUCTURE OF THE OVARY

The ovary is long, inferior, bicarpellary and syncarpous with an indefinite number of anatropous unitegmic ovules borne on a massive

axile placenta. The anterior carpel is distinctly larger than the posterior (Fig. 58). The ovary is bilocular in the lower region but becomes unilocular at the apex (Figs. 57–60). This is due to the incomplete extension of the septum or perhaps its dissolution in the upper region of the ovary (Fig. 61). Correspondingly, placentation is axile in the lower region (Fig. 58) and free central above (Figs. 57b and 59). In *Stylidium adnatum* (Rosén, 1935) one of the chambers becomes atrophied resulting in a unilocular condition. The tendency towards a unilocular condition, also seen in some of the Lobeliaceae, is very significant since it points the way towards the unilocular ovary of the Compositae.

The ovary wall also undergoes certain changes during the development of the ovule into the seed. At the megaspore tetrad stage it is made up of six to seven layers of cells. Those towards the inside are much smaller and the subepidermal layer is filled with densely staining contents (Fig. 62). At the mature embryo sac stage the number of layers increases and the epidermis becomes prominent (Fig. 63). During the early stages of endosperm development the inner three or four layers become lignified (Figs. 64–65) and in the mature fruit a heavy cuticle is deposited over the outer surface.

MEGASPORANGIUM AND FEMALE GAMETOPHYTE

The ovule appears as a conical outgrowth on the placenta. Various stages in its development are presented in Figs. 66 to 71. The integument (Fig. 73) appears immediately after the differentiation of the hypodermal archesporial cell (Fig. 72), and is made up of three layers of cells (Fig. 68). Later it becomes four to five-layered (Figs. 70, 71) except in the micropylar region where the number of layers is larger (Figs. 69 to 71).

There is usually a single hypodermal archesporial cell (Figs. 72, 73) which functions directly as the megaspore mother cell (Fig. 74). Tetrad formation (Figs. 75, 78) takes place normally and the chalazal megaspore is functional. Occasionally a T-shaped tetrad may be found (Fig. 79) as in *Cephalostigma Schimperi* (Kausik and Subramanyam 1947a). Sometimes, the upper dyad cell undergoes a belated division (Fig. 77) as in *Lobelia pyramidalis* (Subramanyam, 1949), or the division is oblique (Fig. 76), as recorded also in *Stylidium adnatum* (Rosén, 1935), *Cephalostigma Schimperi* (Kausik and Subramanyam 1947a) and *Wahlenbergia gracilis* (Subramanyam, 1948). The nucleus of the functional megaspore undergoes three successive divisions (Figs. 84, 85) to produce an eight-nucleate embryo sac of the Polygonum type (Maheshwari, 1948).

Sometimes two megaspore mother cells may be seen in the same nucellus (Fig. 80). Usually both of them develop further forming a double dyad (Fig. 81) and a double tetrad (Fig. 83), or one may slightly lag behind the other (Fig. 82). A similar feature has also been recorded in certain members of Goodeniaceae (Rosén, 1946).

During further development all cells of the nucellar epidermis are destroyed. As a result the mature embryo sac comes in direct contact with the innermost layer of the integument which becomes modified to form the endothelium (Fig. 87). It consists of transversely elongated vacuolate cells with dense contents and conspicuous nuclei. In *Stylidium*

squamellosum Burns (1900) reported a glandular nutritive tissue formed below the antipodal end of the sac. However, neither Rosén (1935) mentions it nor have I been able to observe its presence.

The eight-nucleate embryo sac (Figs. 86 and 87) tapers towards both ends. The synergids are longer than in most plants (Fig. 87). They have a hooked apical end and a broad vacuolate lower portion. In *Stylidium adnatum* (Rosén, 1935), too, the synergids are very long and reach almost to the center of the embryo sac. The egg is pear-shaped and situated between the synergids. As in *S. adnatum*, the two polar nuclei fuse in the center of the embryo sac to form the secondary nucleus just prior to fertilization. The antipodals are organized into definite cells (Figs. 87, 88). Burns (1900) says "kurz nach der Befruchtung sehen wir die Antipoden zu Grunde gehen." In *S. adnatum* (Rosén 1935) and *S. graminifolium*, however, the antipodals persist during the early stages of endosperm development (Figs. 91–95). This feature is also seen in members of the Campanulaceae (Kausik and Subramanyam 1946b) and Lobeliaceae (Kausik and Subramanyam 1946b).

There is a tendency for the lower end of the embryo sac to grow past the antipodals as a very small delicate process (Fig. 88) penetrating the chalazal end. This phenomenon is particularly well seen in some species of *Lobelia* (Kausik, 1938; Subramanyam, 1949).

The mature embryo sac shows a large number of starch grains (Fig. 87), as reported by Burns (1900). They usually appear after the fusion of the two polar nuclei and persist during the early stages of endosperm development (Figs. 92–95) being crowded around the nucleus of each endosperm cell (cf., *Cephalostigma Schimperi*, Kausik and Subramanyam 1947a).

Fig. 89 illustrates a peculiar embryo sac with two antipodal cells at the chalazal end one of which is rather bulbous and the other elongated like an egg. A group of three nuclei occupies the center of the embryo sac. Two of these are of the same size and must be interpreted as

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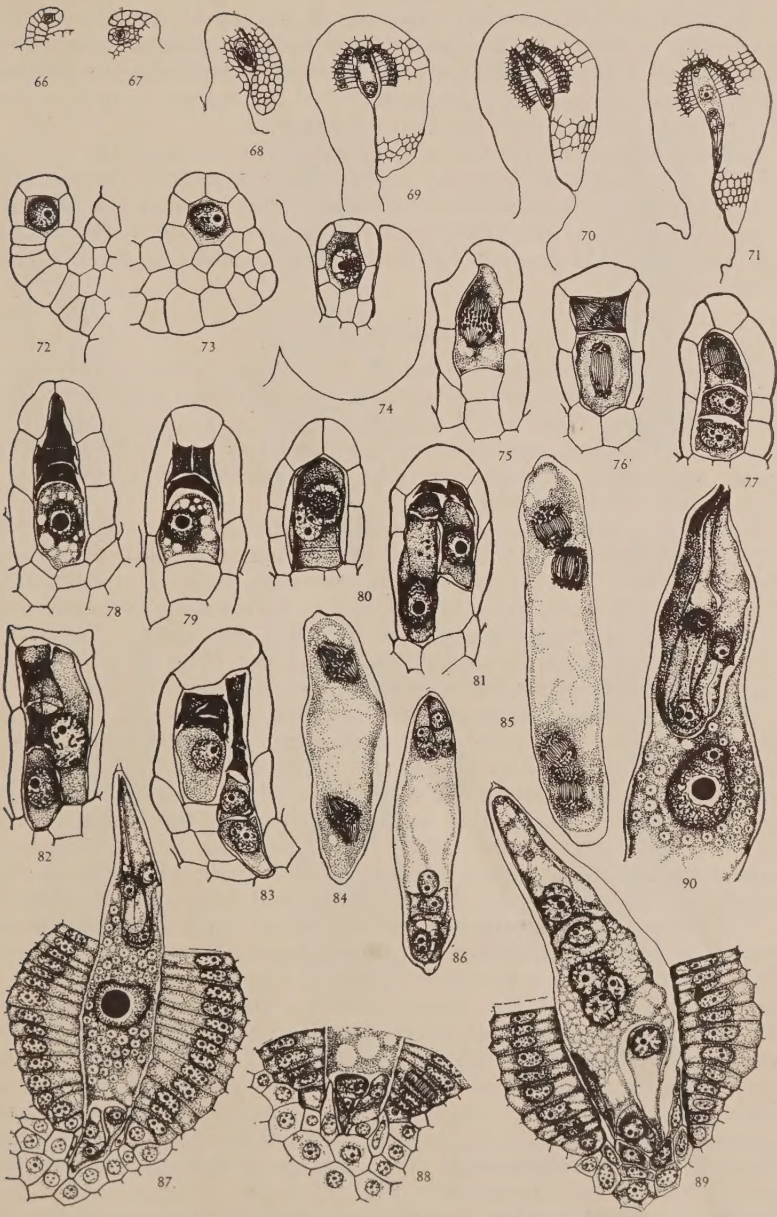
EXPLANATION OF FIGURES

FIGS. 66–71. Stages in development of the anatropous ovule. × 112 each. FIG. 72. L. S. young nucellus showing primary archesporial cell. × 422. FIG. 73. Slightly older stage showing the primordia of the integument. × 422. FIG. 74. Megaspore mother cell. × 422. FIG. 75. Megaspore mother cell in division. × 590. FIG. 76. Dyad cells dividing; note oblique division in upper dyad cell. × 590. FIG. 77. Division in lower dyad cell completed; upper dyad cell in late telophase stage. × 590. FIG. 78. Tetrad of megaspores. × 590. FIG. 79. T-shaped tetrad. × 590. FIG. 80. Nucellus showing two megaspore mother cells in s superposed condition. × 590. FIG. 81. A megaspore tetrad and a dyad lying side by side. × 590. FIG. 82. A megaspore tetrad lying by the side of a megaspore mother cell. × 590. FIG. 83. Two megaspore tetrads lying side by side. × 590. FIGS. 84–85. Second ana third nuclear divisions in the embryo sac. × 590 each. FIG. 86. A young eight nucleate embryo sac. × 422. FIG. 87. Mature embryo sac showing the elongated synergids and the conspicuous integumentary tapetum; note the presence of starch grains in the embryo sac. × 422. FIG. 88. Basal portion of an embryo sac, showing the very small chalazal process, pointed antipodal cells, and conspicuous integumentary tapetum. × 422. FIG. 89. An abnormal embroy sac; for explanation see text. × 422. FIG. 90. A stage in double fertilization. × 422.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the polar nuclei. The third nucleus is smaller and probably represents the nucleus of the remaining antipodal cell. In the two antipodals at the chalazal end of the embryo sac, the nuclei are situated towards the upper ends of the cells and this is particularly clear in the egg-like antipodal cell. It is possible that the cell-wall of the remaining antipodal cell was dissolved and the nucleus migrated further up so as to come to lie in close proximity with the two polar nuclei.

The pollen tube enters the embryo sac between one of the synergids and the wall of the embryo sac so that both synergids remain intact (Fig. 90). Sometimes the pollen tube also enters between the synergids. Double fertilization takes place normally and immediately after fertilization both synergids gradually shrivel and degenerate as in *S. adnatum* (Rosén, 1935).

ENDOSPERM

The primary endosperm nucleus which lies in the center of the embryo sac divides much earlier than the fertilized egg, resulting in the formation of (Fig. 91) a micropylar and a chalazal chamber. A vertical wall is then laid down in the former (Fig. 92) followed by a similar wall in the primary chalazal chamber (Fig. 93) as shown by Rosén (1935) in *S. adnatum.*

Transverse walls are next formed in each of these two tiers, first in the upper tier (Fig. 94) and then in the lower (Fig. 95), as in *Lobelia amoena* (Hewitt, 1939), *L. trigona* (Maheshwari, 1944), *L. nicotianaefolia* (Kausik and Subramanyam, 1946a), and *L. pyramidalis* (Subramanyam, 1949), belonging to the closely allied family Lobeliaceae. This is soon followed by a similar division in the lower tier (Fig. 95). The result is an eight-celled endosperm made up of four tiers of two cells each.

At the eight-celled stage of the endosperm, the two cells of the upper tier develop into the micropylar haustorium and the lower into the chalazal haustorium (Fig. 96). By further divisions the two middle tiers form the main body of the endosperm, which later becomes packed with starch grains (Fig. 100). A similar type of endosperm development has been shown by Rosén (1935) for *S. adnatum* and also occurs in various species of the genus *Lobelia* (Hewitt, 1939; Maheshwari, 1944; Kausik and Subramanyam, 1945a, 1946a; and Subramanyam 1949).

The micropylar haustorium is two-celled, each cell containing a prominent nucleus embedded in a dense mass of vacuolate cytoplasm (Figs. 96, 97). It now becomes lodged in a large cavity formed in the micropylar region of the integument by the enormous micropylar growth of the embryo sac, as reported by Burns (1900) and Rosén (1935) for other members of the Stylidiaceae (Figs. 92 to 96). This feature is seen during the early stages of the *ab initio* cellular endosperm development. Up till this stage the micropylar haustorium resembles that of *S. adnatum* (Rosén, 1935), but in later stages, it develops lateral processes (Fig. 97, *m.p*), which descend down and grow between the parenchymatous cells of the integument (Fig. 98, *m.p*). Such a tendency has also been noticed by Crété (1942) in certain members of the Orobanchaceae and Plantaginaceae. The micropylar haustorium remains active until a very late stage in the development of the seed. The chalazal haustorium is also made up of two uninucleate cells the margins

of which present a lobed appearance (Fig. 96). It reaches almost the base of the seed, disorganizing all cells in the chalazal region of the ovule. Rosén (1935) reports that in *S. adnatum* the chalazal haustorium does not reach such proportions as the micropylar haustorium and becomes atrophied. In *S. graminifolium*, however, the chalazal haustorium,

FIGS. 91–96. Stages in the development of the endosperm and the differentiation of the micropylar and chalazal haustoria. All × 422, except Fig. 96, × 254.

too, is aggressive and both of its cells form a number of processes, which extend between the cells of the integument (Figs. 99, 100, *c.p.* and 101). Crété (1942) reports a similar feature in *Catalpe Kaempferi*. Here the chalazal haustorium sends ramifications between the cells of the hypostase.

SEED COAT

In a mature seed the cells of the outer epidermis and of the integumentary tapetum become filled with a darkly staining material (Fig. 100). The remaining layers of the integument remain clear and

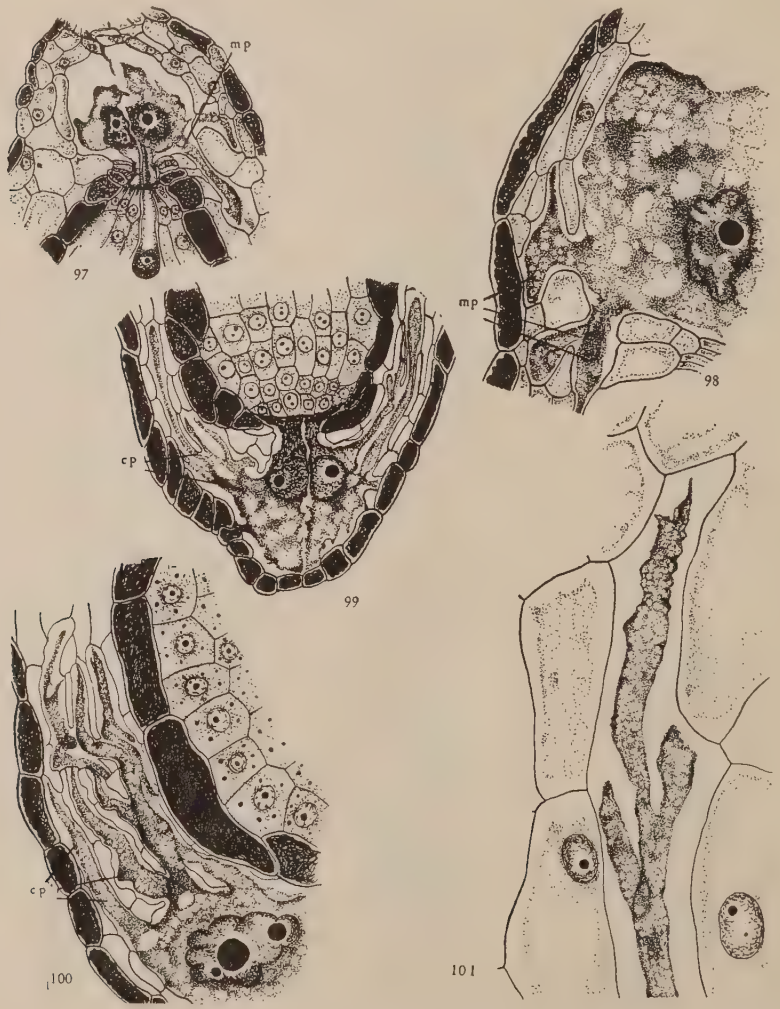
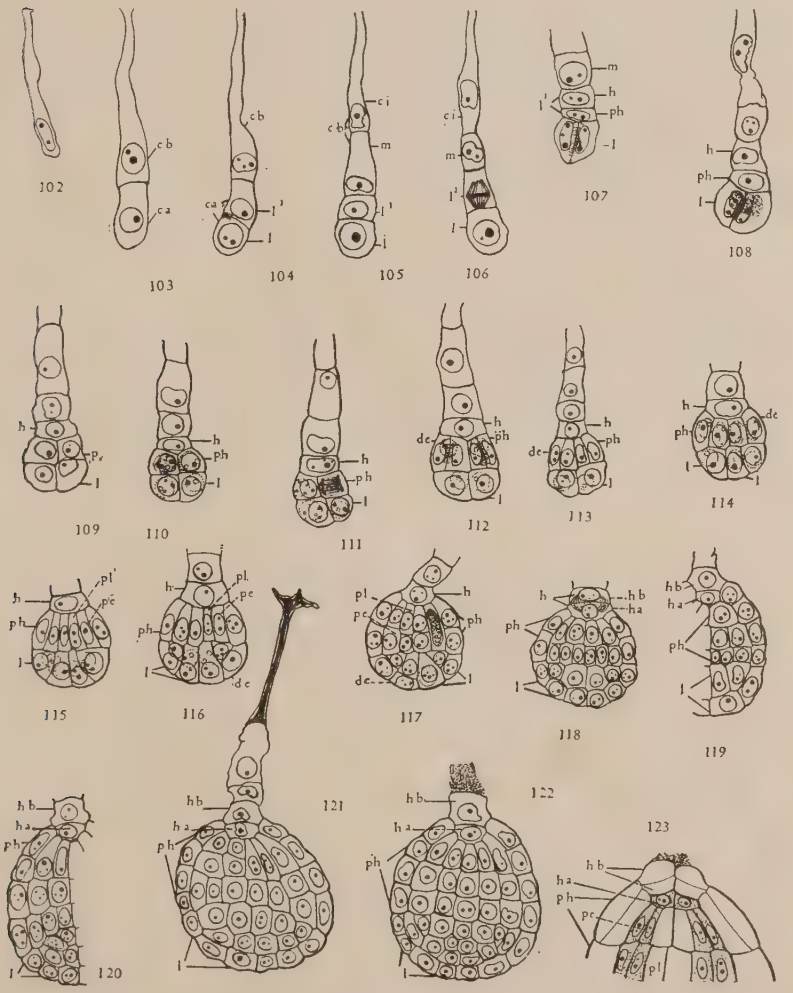


FIG. 97. Two-celled micropylar haustorium; note a process (*m. p.*) from one of the cells of the micropylar haustorium passing into the integument on one side. × 112. FIG. 98. A portion of one of the cells of the micropylar haustorium enlarged to show the hypertrophied nucleus and the processes (*m. p.*) from one of the cells of the micropylar haustorium. × 234. FIG. 99. Two-celled chalazal haustorium giving out processes (*c. p.*) into the integument. × 112. FIG. 100. Portion of one of the cells of the chalazal haustorium enlarged to show the hypertrophied nucleus and the processes (*c. p.*) passing up into the integumentary tissue. × 234. FIG. 101. A branched process from one of the cells of the chalazal haustorium, passing up in between the cells of the integument.

thin-walled. In *S. adnatum* (Rosén, 1935) all cells of the integument are gradually used up except the outermost layer.

EMBRYO

The fertilized egg (Fig. 102) elongates to form a narrow tubular structure which divides by a transverse wall to form cells *ca* and *cb* (Fig. 103). Similar transverse walls are laid down in both daughter



FIGS. 102–122. Stages in the development of the embryo. (*ca* = terminal cell of two-celled embryo; *cb* = basal cell of two-celled embryo; *m* and *ci* = cells derived from the basal cell *cb; 1* = lower daughter cell of *ca; 1'* = upper daughter cell of *ca; ph* and *h* = daughter cells of *1'; ha* and *hb* = daughter cells of *h; de* = dermatogen; *pe* = periblem; *pl* = plerome). × 254 each. FIG. 123. Basal portion of a fairly mature embryo enlarged to show the cells destined to give rise to root cap, dermatogen, periblem (stippled) and plerome. × 254.

cells *ca* and *cb* resulting in the formation of a long and slender proembryo consisting of four cells, *1*,*1*^{1},*m*, and *ci* (Figs. 103–105). Cell *1*^{1} now divides transversely (Fig. 106) producing *ph* and *h* (Fig. 107), whereas *1* divides by a vertical wall (Fig. 107) followed by the development of a similar vertical wall in *ph* (Fig. 109). The four cells thus formed divide by a second set of vertical walls at right angles to the first (Figs. 108, 110).

At the octant stage of the embryo oblique walls arise to form the dermatogen *de* and, after further divisions, the periblem *pe* and plerome *pl* are also differentiated (Figs. 111–117). At this stage the embryo assumes a spherical shape and the third cell *h* divides transversely producing *ha* and *hb* (Figs. 118 to 122). The embryo proper is thus formed by cells *1*, *ph*, *ha*, and *hb*, while the rest of the cells constitute the suspensor (Figs. 121–123).

Cell *ha* undergoes a vertical division and completes the periblem (Fig. 123, stippled part). Cell *hb* also divides anticlinally followed by a transverse division resulting in a group of four cells (Fig. 123). Of these the two inner cells complete the dermatogen; the two outer cells along with the outer cells formed by the periclinal divisions of the basal dermatogen cells form the root cap. The development of the embryo thus conforms to the Solanad type (Johansen, 1945), also met with in members of the closely allied families Campanulaceae (Souéges, 1936, 1938, Kausik and Subramanyam 1947b; Subramanyam, 1948 and Crété, 1948) and Lobeliaceae (Crété, 1938; Hewitt, 1939; Kausik, 1935, 1938; Kausik and Subramanyam, 1945b and 1947b; and Subramanyam, 1949), although there are certain minor differences between them.

CONCLUSIONS

The family Stylidiaceae is interesting because of its discontinuous geographical distribution, peculiarities of floral structure, and other aspects. It resembles the Lobeliaceae in having zygomorphic flowers and subconfluent anthers though in the *Lobeliaceae* the anthers are typically syngenesious. The inferior ovary in both is primarily syncarpous and bilocular, with a tendency towards the unilocular condition found in the Compositae. The presence of nectaries at the apex of the ovary is a further point of similarity between Stylidiaceae and Lobeliaceae.

Embryologically, the Stylidiaceae and Lobeliaceae resemble each other in the following respects. The endothecium is fibrous and the tapetal cells are binucleate. The mature pollen grain is trinucleate consisting of two male cells and a large generative nucleus. Occasionally, the pollen grains show a precocious tendency to germinate within the anther loculus. The embryo sac conforms to the Polygonum type and is surrounded by a conspicuous endothelium. It develops a small process at the chalazal end. The endosperm is cellular and develops according to the Scutellaria type of Schnarf (1931). Embryo development follows the Solanad type (Johansen, 1945).

While admitting that there are certain differences between Stylidiaceae on the one hand and the Campanulaceae and Lobeliaceae on the other, Rosén (1935, 1937) suggests that the Stylidiaceae and Goodenia-

ceae may have originated from Lobeliaceous forms. The former show a one-chambered ovary, elongated synergids, rather persistent antipodals, and a tendency for the chalazal haustorium to become arrested at an early stage. These tendencies are also found in the Compositae and this family is no doubt related to the Lobeliaceae.

The Stylidiaceae have certain special features of their own both in flower structure and embryology. The flower is peculiar in having a structure called the column which represents the fused style with the stamens. Only two stamens are present and the anterior petal is modified into a specialised labellum. The outer surface of the floral parts is covered by a number of stalked multicellular glands, particularly in the genus *Stylidium*. The anther shows a distinct stomium and the endothelium is specially well-developed. Occasionally two megaspore mother cells are formed and these show a tendency to develop further up to the tetrad stage. Both the micropylar and chalazal haustoria are aggressive and form branches which grow in between the cells of the integument. This can be regarded as a special type of nutritive mechanism in the development of the seed.

SUMMARY

The floral parts take their origin in acropetal succession. There is a marked tendency for the anterior part of the flower to precede the posterior in development. Multicellular stalked glands are present on the axis of the inflorescence and on the outer portions of the floral parts except the column. They are epidermal in origin and their development has been described in detail.

The wall of the anther consists of three layers of cells external to the tapetum. The tapetal cells are binucleate and the endothecium shows the usual fibrous thickenings. The pollen grains are three-celled and sometimes germinate *in situ*. They show five prominent bands and the exine is closely and finely echinulate.

The ovary is inferior and bilocular, the anterior locule being usually larger than the posterior. The bilocular ovary becomes unilocular at the top and encloses an indefinite number of anatropous, unitegmic ovules borne on an axile placenta. At the base of the column occur two nectaries, the anterior being larger than the posterior. The innermost layer of the integument forms a very conspicuous endothelium. During post-fertilization stages the inner layers of the ovary wall become strongly lignified.

There is usually a single archesporial cell which directly functions as the megaspore mother cell. Occasionally two megaspore mother cells are found and these develop as far as the tetrad stage.

Megasporogenesis proceeds normally and the embryo sac is of the Polygonum type. The synergids are elongated and show characteristic hook-like projections. The antipodal cells are pointed at their lower ends and the embryo sac develops a small process which protrudes beyond them. Double fertilization has been observed.

The endosperm is cellular and its development corresponds to the Scutellaria type of Schnarf (1931). The micropylar haustorium is made up of two uninucleate cells and the chalazal haustorium is also two-

celled. Both are aggressive and develop prominent tubular branched processes which protrude between the cells of the integument.

The development of the embryo follows the Solanad type of Johansen.

Therefore, the family Stylidiaceae is closely related to the Lobeliaceae.

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POSTSCRIPT

When this study was about to be submitted for publication, I received a paper by Rosén (1949) entitled "Endosperm development in Campanulaceae and closely related families." In this paper he presented some features on the embryology of two members of this family, viz., *Stylidium graminifolium* and *S. caespitosum*. He showed that in these forms the cells of the integumentary tapetum are a little broader than those of *S. adnatum* studied by Burns (1900). The synergids are elongated and reach a long way into the micropyle. The antipodal cells persist even during the early stages of endosperm development. Endosperm development follows the Codonopsis type. The haustoria are delimited at the eight celled stage of the endosperm and the chalazal haustorium is considerably smaller than the micropylar.

The Genus Luxemburgia (Ochnaceae)

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The fact that the 16 species of the ochnaceous genus *Luxemburgia* are confined to three States of southeastern Brazil: Minas Geraës, Rio de Janeiro, and Bahia, and are represented in herbaria by few collections, makes it easy to understand why these shrubs are little known to taxonomists. The genus, however, is the type of the New World and Old World tribe Luxemburgieae encompassing such well-known, althoughly relatively small, tropical American genera as *Cespedezia*, *Sauvagesia*, and *Lavradia*.[1] In addition other smaller genera of the tribe have been restudied or described as new during the past twenty-five years as a result of the botanical exploration of the sandstone mesas of Roraima, Duida, and Auyantepui of the Pacaraima Range of mountains of the Venezuela-British Guiana Border, as well as a survey of the Tafelberg and Kaieteur plateaus in Central Surinam. Such genera as *Leitgebia* Eichl., *Philacra* Dwyer, *Tyleria* Gleason, and *Poecilandra* Tulasne have been collected on one or several of these mesas. *Philacra*, a close relative of *Luxemburgia*, with two of its three species known only from collections on Mount Duida, demonstrates the importance of intergeneric study. *Tyleria*, described in 1931, has four clear-cut species known only from Mount Duida. While it is not as closely related to *Luxemburgia* as *Philacra*, nevertheless it has served to broaden our interpretation of the entire tribe.

History of the Genus Luxemburgia

In 1915 Beauverd (2) presented an historical resume of the Luxemburgias, thus making a lengthy discussion unnecessary. St. Hilaire (8) first described the genus *Luxemburgia*, dedicating it to the Duke of Luxembourg, French ambassador to Brazil in 1816. It was under his patronage that St. Hilaire explored the country in and around Rio de Janeiro from 1816 to 1822. St. Hilaire placed the newly described genus, together with *Sauvagesia* L. and *Lavradia* Vell., in the Frankeniaceae. Planchon (7) was the first to place the genus in the Ochnaceae as the type genus of the tribe Luxemburgieae (Section apud Planchon), a grouping subsequently maintained by Bentham & Hooker (3), Baillon (1), and Engler (4, 5). Walpers (10), on the other hand, placed the genus in the Sauvagesieae. Van Tieghem (9) introduced more radical changes by dividing the genus into five genera and making it the type genus of the family Luxemburgiaceae. Beauverd (loc. cit.) subsequently reduced these genera as sections of the genus *Luxemburgia*, accepting

[1]This paper represents a segment of a thesis on the *American Genera of the Tribe Luxemburgieae* (Ochnaceae), submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, Biological Laboratories, Fordham University Graduate School, New York, N.Y.

Gilg's (6) division into the natural and clear-cut Epetiolatae and Petiolatae sections.

I have discussed the position of the genus *Luxemburgia* in the Tribe Luxemburgieae in several papers.[2] While the reader is referred to these papers for a further discussion, I would like to point out that *Luxemburgia* [and the closely related *Philacra*, endemic to the Sierra Pacaraima Range of Northern South America], are readily distinguished from all of the other genera of the Tribe by the character of their androecium; the connate anthers are disposed in a half to three quarter circle around the pistil, the short filaments being persistent in the fruit (Fig. 1, b–c).

Fig. 1. Luxemburgia St. Hil. *L. Damazioana* Beauverd: a—bud (× 2); b—flower (× 2); c—longitudinal section through flower (× 4); d—stamen, showing a single stamen attached to a portion of the connate-filament mass (× 5); e—apical portion of anther, dorsal view, showing dehiscence (× 10); f—apical view of anther showing the two terminal pores (× 10); g—capsule (× 1); h—seed (× 20); j—leaf (× 1). (a—f, drawn from *Mello 6151;* g—j, drawn from *Mello* and *Brade 1235*).
L. elegans Dwyer: k—leaf (× 1). (drawn from *Claussen 5A*, TYPE).

ACKNOWLEDGMENTS

Specimens cited in this paper are deposited in herbaria of the institutions listed below, the customary symbol being used to designate the particular institution.

Chicago Natural History Museum (F).
Gray Herbarium (G).
Royal Botanic Garden (K).
New York Botanical Garden (NY).
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United States National Herbarium (US).

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The symbol s.no. is used in citing specimens without a collection number. I wish to express appreciation to the directors of the above institutions who by their cooperation made this study possible. Special thanks are due to Dr. A. C. Smith for his advice and to Dr. Charles Gilly who prepared the plate and made valuable suggestions.

KEY TO THE SPECIES

Leaves epetiolate.....Section 1. EPETIOLATAE
  Flowers numerous in a terminal raceme.
    Leaf-blades oblong, obovate or obovate-lanceolate (more than 1 cm. wide).
      Costa of leaf-blades obviously not plane.
        Bracts shorter than sepals.
          Sepals equal or subequal, scarcely imbricate at anthesis, lanceolate to oblong.....1. *L. octandra.*
          Sepals unequal, imbricate at anthesis, oblong to rotund.
            Secondary veins on upper surface of lamina plane; margins of sepals densely ciliate above middle; pedicels of flowers up to 7 mm. long; stamens 20–40.....2. *L. elegans.*
            Secondary veins on upper surface of lamina elevated; margins of sepals sparsely ciliate above middle; pedicels of flowers 1.7–2 cm. long; stamens 12–20 (rarely 30).....3. *L. nobilis.*
        Bracts longer than sepals.
          Pedicels slender (about 0.8 mm. wide), up to 15 mm. long; sepals non-imbricate at anthesis.....4. *L. Gaudichaudi.*
          Pedicels crassate (about 1.5 mm. wide), 15–40 mm. long; sepals imbricate at anthesis.....5. *L. bracteata.*
      Costa of leaf-blades plane beneath.
        Pedicels about 2 cm. long, 0.1 cm. wide; margins of leaf-blades lacking accessory cilia.....6. *L. Schwackeana.*
        Pedicels about 1.5 cm. long, 0.15 cm. wide; margin of leaf-blades lacking accessory cilia.....7. *L. speciosa.*
    Leaf-blades linear (less than 0.9 cm. wide).....8. *L. angustifolia.*
  Flowers few in a compressed raceme.....9. *L. corymbosa.*
Leaves petiolate.....Section 2. PETIOLATAE
  Leaf- margin uncinate-toothed, not ciliate above base.....10. *L. polyandra.*
  Leaf-margin usually uncinate-toothed, always ciliate above base.
    Leaf-margin not uncinate-toothed.....11. *L. Damazioana.*
    Leaf-margin uncinate-toothed.
      Marginal cilia of leaf-blade not paired.
        Cilia of stipules not villose.
          Leaf-blades oblong, 6–13 cm. long, 2–3 cm. wide, the marginal cilia about 3 mm. long.....12. *L. major.*
          Leaf-blades narrow-elliptic, 3–8 cm. long, 0.8–2 cm. wide, the marginal cilia 1–2 mm. long.....13. *L. Glazoviana.*
        Cilia of stipules villose or subvillose, crowded.
          Leaf-blades 3.5–5 cm. long; costa of leaf-blade plane beneath; articulation-stalk of pedicel about 3 mm. long; sepals 3–9 mm. long.....14. *L. villosa.*
          Leaf-blades about 9 cm. long; costa of leaf-blades prominent beneath; articulation-stalk of pedicel about 15 mm. long; sepals 5–11 mm. long.....15. *L. Gardneri.*
        Cilia on margin of leaf-blade paired.....16. *L. diciliata.*

1. LUXEMBURGIA OCTANDRA St. Hil. Mem. Mus., Paris, **9**:352. 1823.

Plectanthera floribunda Mart. and Zucc. Nov. Gen. **1**: 40. 1824.

Shrubs; leaf-blades persistent and crowded at apex of branchlets, subsessile, elliptic or obovate-lanceolate, up to 8 cm. long, 0.8–1.3 cm. wide, obtuse and vaguely retuse at apex, cuneate or tapering very

narrowly at base, the marginal teeth uncinate, the costa prominent above and below, the secondary veins prominulous; stipules subulate, up to 3 cm. long; inflorescence elongate and racemose, the rachis canaliculate, 5–20 cm. long, the bracts striate, linear (rarely lanceolate), the pedicels slender, up to 1.3 cm. long, the articulation-stalk up to 3 mm. long; flower buds conical, up to 0.75 cm. long; sepals equal or subequal, non-imbricate, narrow-oblong to lanceolate, up to 4.2 mm. long, obtuse or tapering obtusely at apex into glandular apiculum, the marginal cilia extending almost to base, up to 0.5 mm. long; petals unequal, obovate, more than twice length of stamens, obtuse to vaguely retuse with minute apical cilium; stamens 7–20, the anthers up to 3.5 mm. long; ovaries oblong, up to 5 mm. long, longer than rostrate thickened falcate style; capsule subterete, narrow-elliptic, about 1 cm. long at dehiscence, about 0.3–0.4 mm. wide, the seeds oblong, contorted, about 0.9 mm. long, the wing often aborted or about 0.3 mm. long, frequently encircling body of seed.

TYPE LOCALITY: Minas Novas, Minas Geraës, Brazil.
ILLUSTRATION: Bull. Soc. Bot. Genève II. **7**: *pl. 2. f. 2.* 1915.
DISTRIBUTION: Limited to the mountains of southeastern Brazil.

BRAZIL: *Claussen* s. no. (NY); *Riedel* s. no. (NY); *Sellow* s. no. (K); Minas Geraës: *Claussen* s. no. (K); Capanesma, *Claussen* s. no. (NY); Serra D'Ouro, Preto, *Claussen* s. no. (F); without locality, *Claussen 1110* (P); Minas Novas, *St. Hilaire* s. no. (P, type); without locality, *Riedel 255* (K); without locality, *Glaziou 19891* (K, P); Petropolis au Morin, *Glaziou 18331* (P); D'Ouro Preto, *Glaziou 14592* (K), *20247* (K, P); without locality. *Martius 898* (K, NY); Antioquia, *Terrise* s. no. (K); without locality, *Weddell 1204* (P); Morro Velho, *Gardner 4410* (K, NY); Serra do Piedade, *Mello 6152* (F); Nova Lima, *Mello 7780* (F); without locality, *Sello 1998* (P).

L. octandra has been more extensively collected than any other species of *Luxemburgia*. Two combined characters, the non-imbricate sepals and the linear-lanceolate bracts readily distinguish it from the three species of the genus to which it is obviously related: *L. elegans*, *L. nobilis*, and *L. Gaudichaudi*. The non-imbricate sepals separate it from the first two species. The most obvious character serving to distinguish it from *L. Gaudichaudi* is its narrower bracts.

St. Hilaire's type collection was undoubtedly made at Villa Rica, Minas Novas in the State of Minas Geraës, Brazil.[3]

2. **Luxemburgia elegans,** sp. nov.

Suffrutices; laminis foliorum sessilibus gracili-coriaceis apicibus

[3]On the type collection deposited in the Museum Histoire Naturelle (Paris) there is a notation (in St. Hilaire's hand?) that the specimen was collected in Villa Thica. This is undoubtedly a mispelling of Villa Rica. According to St. Hilaire (Hist. Pl. Brés. vol. 1. 1824) Villa Rica is the "capitale de la province des Mines" (Minas Geraes) and is located in the district of Minas Novas. It is interesting to note that St. Hilaire (loc. cit.) has provided us with considerable information concerning the physical character of these areas and the enthnological character of its inhabitants as he observed them in late 1816 to early 1818. We know from his itinerary that he botanized in Villa Rica in Dec.–Jan. of 1816–1817 and again in Jan. of 1818. This information has been made more readily accessible to students by the publication of St. Hilaire's travels in Brazil and Paraguay in vol. 10. no. 1 of *Chronica Botanica* (1946).

ramulorum crebris angusto-lanceolatis vel lineari-obovatis, 5–10 cm. longis, 1–1.3 cm. latis, apice obtusis anguste basi attenuatis, inde in crassum articulationis locum expandentibus marginibus serratis dentibus uncinatis appressis, 1–2 mm. distantibus, costa utrimque prominente venis secundariis subtus planis vel subplanis, supra planis angulo 60° paralleli-ascendentibus, stipulis persistentibus minimis subulatis, circ. 2 mm. longis, vix divisis vel integris; floribus multis in terminalem racemum dispositis rhachidibus ad 12 cm. longis foliis aequalibus, pedicellis crassis recurvatis, circ. 7 mm. longis, circ. 0.5 mm. in medio latis, apice obtusis brevi-ciliatis (cilio longissimo circ. 1 mm. longo); gemmis ovato-oblongis, ad 7 mm. longis, 4 mm. latis; sepalis imbricatis inaequalibus coriaceis dorsaliter ventraliterque striatis, 3 externibus brevioribus rotundis, 2.3–2.8 mm. longis, 2–2.3 mm. latis, apice basique rotundo-obtusis, margine scarioso ciliis crebris ascendentibus ad 0.7 mm. longis; petalis inaequalibus obovato-oblongis, 8–10 mm. longis, 5–6 mm. latis, interioribus 2, 3.3–3.7 mm. longis, 2.3–2.8 mm. latis, apice obtusis, basi obtusis paullum attenuatis; staminibus 20–40, antheris linearibus, 4–5 mm. longis, subanthesi disjunctis, filamentis circ. 0.5 mm. longis; ovariis circ. 0.5 mm. longis, stylo cylindrico, 1.5 mm. longis, stigmatibus scariosis irregularibusque; capsulis (prae dehiscentibus) oblongis, circ. 2.5 mm. longis, seminibus circ. 0.9 mm. longis, ala unilaterale apice semini longitudine aequale (Fig. 1, *k*).

TYPE LOCALITY: Brazil.

DISTRIBUTION: Known only from Brazil.

BRAZIL: without locality, *Claussen 5A* (F, type, G).

This species, although described from material in the mature bud stage, reveals adequate floral characters to separate it from its obvious ally, *L. nobilis*. The margins of the sepals bear densely crowded cilia and the stamens are constantly more numerous. On the basis of vegetative characters, *L. elegans* is readily distinguished from *L. nobilis*. The secondary veins on the upper surface of the lamina are plane, while in *L. nobilis* they are somewhat elevated. The relatively shorter pedicels of the new species furnish a stable differentiating character.

3. LUXEMBURGIA NOBILIS Eichl. in Mart. Fl. Bras. **12** (2): 360. 1876.

Shrubs; leaves sessile, linear-elliptic, linear-lanceolate or narrow-obovate, 3–9 cm. long, 0.7–2.3 cm. wide, acute or flat-obtuse at apex, terminating in a cilium up to 3 mm. long, the margin with small ascending falcate teeth, the costa prominent beneath, the secondary veins prominulous above and below, oblique and parallel-ascending; stipules persistent along branchlets, minute, subulate, divided into a large central cilium with smaller basal cilia; flower-buds oblong, up to 1 cm. long, 0.5 cm. wide; inflorescence terminal, racemose, scarcely exceeding uppermost leaves, the rachis 3–10 cm. long, the bracts usually persistent, linear-lanceolate, 4–5.5 mm. long, the cilia short, oblique-ascending, the pedicels 1.7–2 cm. long, the articulation-stalk 0.2–0.5 cm. long; sepals unequal, rotund (often almost square), oblong to rectangular, 2.8–5.5 mm. long, less than half length of petals, 3–4 mm. wide, imbricate

(at least below middle) at anthesis, obtuse to auriculate at base, the cilia scattered above middle of margin (rarely below); petals wide-oblong or obovate-oblong, 6–11 mm. long, 2.5–6 mm. wide, retuse, often apiculate at apex, obtuse at base; stamens 12–30, the anthers fused, 6–9 mm. long; ovaries narrow-oblong, 3–5 mm. long, about 1.5 mm. wide; capsule turgid at base, somewhat contracted in middle, 8–15 mm. long, 3.5–4.5 mm. wide, the seeds narrow-oblong, about 1.3 mm. long, the wing terminal, 0.6–0.9 mm. long, evanescent below middle of seed.

TYPE LOCALITY: Mt. Itacolumi, Minas Geraës, Brazil.
ILLUSTRATION: Eichl. in Mart. Fl. Bras. **12** (2): *pl. 75.* 1876.
DISTRIBUTION: Apparently well distributed throughout Minas Geraës and Rio de Janeiro, Brazil.

BRAZIL: without locality, *Riedel* s. no. (G); *Sellow* s. no. (K, lower half of sheet); Minas Geraës: *Claussen* s. no. (K, P), *Claussen 1509* (P); *Martius* s. no. (US); *Cassaretto 2598* (P); *Langedorff* s. no. (K); *Riedel 42* (P, on lower half of sheet); *Martius 898* (G, on same sheet with *L. octandra*); Rio de Janeiro: *Glaziou 14593* (K).

Both floral and vegetative characters give evidence of the close relationship existing between *L. nobilis* and *L. octandra*. The strongest floral character linking these is undoubtedly the reduction in the number of stamens in both species. While the compressed inflorescence of *L. nobilis* and its polymorphic and unequal sepals imbricate at anthesis, offer substantial key characters segregating it from *L. octandra*, the variety of leaf-shapes of *L. nobilis* furnish a less critical but useful distinguishing character.

4. LUXEMBURGIA GAUDICHAUDI van Tieghem, Ann. Sci. Nat. VIII. **19:** 4. 1904.

Shrubs; leaf-blades sessile, oblong or obovate-elliptic, up to 8 cm. long, up to 2.5 cm. wide, tapering obtusely or subacutely at apex, the marginal teeth appressed-uncinate, the terminal cilium up to 3 mm. long, the costa prominent above and below, the secondary veins subplane above and below; stipules subulate, up to 4.5 mm. long, the cilia short, perpendicular; inflorescence racemose, the rachis glandular, angular, smooth, up to 14 cm. long, 0.3 cm. wide at base, the bracts marcescent-striate, very conspicuous at apex of rachis, linear-lanceolate, up to 9 mm. long, 1–1.5 mm. wide, a little longer than bracteoles, the midvein distinct, the cilia oblique and well-spaced, up to 0.8 mm. long, the pedicels up to 17 mm. long, slender, about 0.8 mm. wide, the articulation-stalk about 3.5 mm. long; flower buds oblong, up to 9 mm. long; sepals not obviously imbricate, unequal, oblong to lanceolate, 4.5–6.5 mm. long, 2–3 mm. wide, tapering acutely at apex, obtuse to subauriculate at base, short-ciliate almost to base, the cilia subulate and oblique-ascending; petals unequal, subcarnose, obovate-oblong or obovate, up to 9 mm. long, 5–7 mm. wide, rounded and often retuse at apex, round-obtuse and often retuse at apex, round-obtuse or vaguely cuneate at base; stamens numerous; ovaries oblong, about 7.5 mm. long, the style rostrate, up to 2 mm. long; fruit not seen.

TYPE LOCALITY: Minas Geraës, Brazil.
ILLUSTRATION: Bull. Bot. Soc. Genève II. **7:** 243, *pl. 2, f. 1.* leaf, 1915.

DISTRIBUTION: Known only from the State of Minas Geraës, Brazil.

BRAZIL: Minas Geraës: without locality, *Gaudichaud 98* (F, photo and frag. of type of *L. Gaudichaudi*); Serra San João d'El Rey, *Heracelzan* s. no. (K).

On comparing the Kew specimen with the photograph of the type collection deposited in the Chicago Natural History Museum there is no doubt that the two are conspecific. The most conspicuous character of *L. Gaudichaudi*, the large bracts which are conspicuous to the apex of the rachis, shows up clearly in the photograph. This species is readily separated from its closest ally, *L. bracteata* by its much reduced pedicels with a very short articulation-stalk.

5. **Luxemburgia bracteata,** sp. nov.

Suffrutices; cicatricibus foliorum late transversis, 0.5–1.5 mm. longis, circiter 3 mm. latis; laminis foliorum sessilibus obovato-ellipticis, 8.5–10.5 cm. longis, 2–2.5 cm. latis, apice obtusis basi attenuatis marginibus alatis costa utrimque prominente venis secundariis supra prominentibus subtus subplanis, 1.7–2.5 mm. distantibus, dentibus marginis serratis appressis uncinatisque, 1.5–2.5 mm. distantibus; stipulis late subulatis, ad 3 mm. longis, vix divisis medio segmento; floribus paucis in racemum terminalem dispositis rhachidibus ad 8 cm. longis, vix superiora folia excedentibus, pedicellis quadrilangularibus, 1.5–4 cm. longis, apice 1–1.2 mm. latis, loco articulationis a basi ad 16 mm. longo extendente bracteis infra illos striatis, elliptico-lanceolatis, circiter 7 mm. longo ciliis paucis sed saepe prominentibus; stipulis lateralibus dentato-ciliatis minutis bracteis loco articulationis in textura magnitudineque similibus; gemmis crassis ovatis, ad 1.2 cm. longis, ad 0.6 cm. latis; sepalis inaequalibus imbricatis subscariosis irregulare-rotundis, cordatis vel oblongo-rectangularibus, 5–7 mm. longis, circiter 4 mm. latis, apice sinibus retusis ad 1.3 mm. altis, basi obtusis subsaccatis margine subpellucido gracile-scarioso eroso vel raro ciliis ad 0.35 mm. longis, venis prominentibus distantibus suberectis vel leviter ad marginem flabellatis; petalis obovato-rotundis, circiter 1.4 cm. longis, 1–1.2 cm. latis, apice retusis sinibus ad 1.3 mm. altis, specie bilobatis; staminibus 50, antheris circiter 10 mm. longis, pistillis transverse triangularibus stylis circiter 2 mm. longis; capsulibus 2–2.5 cm. longis, circiter 2 mm. latis in medio, placentis asperibus, circiter 2.5 mm. latis, seminibus non visis.

TYPE LOCALITY: São João D'Ouro Preto, Minas Geraës, Brazil.

DISTRIBUTION: Known only from the type locality.

BRAZIL: Without locality, *Sello* s. no. (K); Minas Geraës: São João, D'Ouro Preto, *Glaziou 18781* (K, type of *L. bracteata*, P).

This species, named for its conspicuous bracts, is closely related to *L. Gaudichaudi*. As mentioned previously, the latter species has much reduced pedicles with a short articulation-stalk. The pedicels of *L. bracteata* are not only more elongate but are also more stout. Other striking differences are: the secondary veins of the leaf-blades of *L.* bracteata are prominent on the upper surface while those of *L. Gaudichaudi* are subplane on the upper surface; the rachis of the inflorescence of *L. bracteata* is shorter and the inflorescence itself more compressed; the buds are larger, the sepals are retuse as opposed to the acute character of those of *L. Gaudichaudi*, and the petals are obviously larger.

6. LUXEMBURGIA SCHWACKEANA Taub. Bot. Jahrb. **17**: 504. 1893.
Periblepharis Schwackeana (Taub.) van Tieghem, Jour. de Bot. **16**: 290. 1902.

Shrubs; leaf-scars oval, about 2 mm. long, 1 mm. wide; leaf-blades sessile, stiff-coriaceous, oblong to obovate, 1.3–4.5 cm. long, 0.8–1.5 cm. wide, obtuse (and vaguely retuse) at apex, terminating in a cilium up to 3 mm. long, subtended by smaller cilia, cuneate at base, the costa prominent above, plane beneath, the secondary veins visible above and below, 1–1.5 mm. apart, arcuate-ascending at about 55° angle from costa, the marginal teeth short and blunt with or without a marginal perpendicular cilium (up to 1.3 mm. long) between the teeth; stipules persistent, lanceolate, up to 1 cm. long, dissected into numerous divergent elongate cilia, basally fimbriate, a single cilium obvious on each side of a leaf-scar; flowers not seen; fruit borne on a short terminal rachis, the pedicels stout, lignose, black, distinctly angular and carinate, about 1.5 cm. long, the persistent style about 0.25 mm. long, the seeds plump, roughly 3-angled in cross-section, oblong, reticulate, about 1 mm. long, the terminal wing about 0.25 mm. long.

TYPE LOCALITY: Biribiry, Diamantina, Minas Geraës, Brazil.

ILLUSTRATION: Bull. Bot. Soc. Genève II. **7**: *pl. 1, f. 2 a and b.*, leaf, 1915.

BRAZIL: Minas Geraës: Biribiry, Diamantina, *Glaziou 18978* G, photo of type of *L. Schwackeana;* K, cotype collection), *Glaziou 18978* (F, G, photos, P, cotype collection of *L. Schwackeana* and *L. Taubertiana*, left hand side of sheet).

Gilg in his relatively recent review (6) of the Ochnaceae described a new species *L. Taubertiana*, using as a cotype *Glaziou 18979*, which Taubert had established as the cotype of his species *L. Schwackeana*. Gilg considered the hitherto uncited *Schwacke 8109* to be conspecific and cotypic with *Glaziou 18979*. Both, he states (loc. cit.), differ from the other cotype of *L. Taubertiana* in the marginal teeth of the leaves laking intermediate cilia. Although Gilg states very clearly that *Glaziou 18979* lacks intermediate cilia, and regards ciliation as being a constant character, critical examination of the Glaziou collection *18979* deposited in Kew Gardens, shows that marginal cilia are present on many of the leaf-blades. The fact that this specimen bears a tag with numbers corresponding to the label seems to indicate that there has been no confusion in numbers. Therefore there seems to be no reason for segregating *L. Taubertiana* as a distinct species.

7. LUXEMBURGIA SPECIOSA St. Hil. Hist. Pl. Brés. **1**: 333. 1824.

Shrubs; leaf-blades sessile, obovate-lanceolate or oblong, up to 4.6 cm. long, 1.7 cm. wide, obtuse at apex, cuneate at base, the serrate margin with crowded and vaguely uncinate teeth, the costa rubescent, 0.8 mm. wide at base, subplane above, plane beneath (except toward base), the secondary veins plane above, scarcely visible below, ascending at 55°–50° from costa, 1.3–1.9 mm. apart in middle of lamina; stipules persistent, subulate, up to 9 mm. long; inflorescence racemose the rachis scarcely exceeding the tips of leaf-blades, the bracts striate, lanceolate, up to 6 mm. long, the stipules at least one-half length of bracts, the bibracts somewhat shorter and long-stipulate, the pedicels crassate,

about 1.5 cm. long, 0.15 cm. wide, the articulation stalk 1–4 mm. long; flower buds large, ovate, 1–1.3 cm. long, 0.7–0.8 cm. wide; sepals unequal, ovate to oblong, 5–7 mm. long, 4–5 mm. wide, obtuse and retuse (often irregular) at apex, usually auriculate at base, the marginal teeth weak and minute; petals obovate, up to 14 mm. long, obtuse at apex; anthers up to 8.5 mm. long; ovaries narrow-oblong, about 8 mm. long; capsule ovate, up to 1.3 mm. long.

TYPE LOCALITY: Mountains near Milhoverde, Minas Geraës, Brazil.
ILLUSTRATION: St. Hil. Hist. Pl. Brés. **1**: *pl. 29.* 1824.
DISTRIBUTION: Known only from the type collection.

BRAZIL: Minas Geraës: Milhoverde, *Saint Hilaire* s. no. (P, type collection of *L. speciosa*).

Although this description is based solely upon the type material, the specific characters seem to separate it clearly from the other species of the Epetiolatae section. While its plane costa and markedly elongate and densely ciliate stipules point to its affinity with *L. Schwackeana*, its compressed inflorescence with the flowers borne on shorter pedicels and the stipules being scarcely lacinate-ciliate indicate its distinctness as a species. Although the description of the inflorescence of *L. speciosa* has been made from material in the bud stage and that of *L. Schwackeana* from sterile material, there seems to be no doubt that the two species have the largest flowers and fruits of the members of the genus.

8. LUXEMBURGIA ANGUSTIFOLIA Planch. Lond. Jour. Bot. **5**: 596. 1846.

Shrubs; lenticels oblong, 1.9–2.8 mm. long, a single one above each leaf-scar; leaves sessile, linear, up to 9 cm. long, up to 0.9 cm. wide, acute at apex, tapering narrowly at base, the marginal teeth uncinate or erect, the costa red, prominent above and below, the secondary veins scarcely prominent, often irregular-ascending from costa at about 45° angle; stipules persisting along most of ultimate branches, up to 6 mm. long, the corpus divided into 3 subulate and villose segments; inflorescence racemose, the flowers loosely arranged, the rachis up to 6 cm. long, the bibracts linear, about 4 mm. long, sparsely ciliate, those at articulation-joint somewhat smaller and subtended by coiled cilia, the pedicels slender, arcuate-ascending, up to 3 cm. long, the articulation-joint about 0.6 cm. above base; flower buds oblong, up to 8 mm. long; sepals unequal, imbricate, vaguely carinate, oblong or ovate, 3–4.5 mm. long, about 2 mm. wide, obtuse to subacute at apex, auriculate or obtuse at base, the margin entire (except with cilium at apex); petals wide or narrow-obovate, 10–11 mm. long, 5.5–7.5 mm. wide, obtuse and entire at apex, cuneate at base; stamens up to 5.5 mm. long; ovaries lanceolate, up to 8 mm. long, the style very short and suberect; capsule oblong, 1–1.5 cm. long, about 0.6 cm. wide, flat-obtuse at apex (before dehiscence), apiculate, the body of seeds plump, vaguely reticulate, oblong 1–1.2 mm. long, the wing rounded and extending 0.25 mm. (rarely up to 0.45 mm.) beyond apex of body and tapering laterally toward base.

TYPE LOCALITY: Diamantina, Minas Geraës, Brazil.
ILLUSTRATION: Beauv. Bull. Soc. Bot. Genève II. **7**: *pl. 1, f. 1*, 1915.
DISTRIBUTION: Apparently restricted to the State of Minas Geraës, Brazil.

BRAZIL: Minas Geraës: Diamantina, *Gardner 4412* (G, photo of type of *L. angustifolia*, K type, US); without locality, *Riedel* s. no. (G, K, US).

L. angustifolia is very readily recognized by its constantly narrow and linear leaf-blades and its slender pedicels which are disposed in the form of an umbel in the pressed specimen.

9. LUXEMBURGIA CORYMBOSA St. Hil. Hist. Pl. Brés. **1**: 335. 1824.

Subshrubs 2–3 m. high; petioles about 3 mm. long; leaf-blades few at apex of branchlets, linear-obovate, up to 4.3 cm. long, up to 1.5 cm. wide, becoming acute at apex, narrow-cuneate at base, the marginal teeth minute and falcate, up to 1 mm. apart, the costa prominent above and below, the secondary veins prominulous above and below, about 1 mm. apart, ascending at about a 70° angle and enclosing smaller sublateral veins, the latter parallel and eventually reticulate; stipules persistent, subulate, up to 4.2 mm. long, villose-ciliate; inflorescence compressed-racemose, the flowers 3–4, the bracts linear, the margins involute, the cilia well-spaced, oblique-ascending, about 0.5 mm. long, the pedicels up to 2 cm. long, not exceeding leaf-blades in length, the articulation-stalks up to 2 mm. long; sepals unequal, ovate to oblong, 7–12 mm. long, 4–6 mm. wide, acuminate at apex, mostly auriculate at base, the marginal teeth minute, uncinate or simply obtuse; petals unequal, obovate-rotund, up to 18 mm. long, 14 mm. wide, rounded and apiculate at apex, obtuse to cuneate at base; anthers up to 6.5 mm. long; ovaries 6 mm. or more long; fruit not seen.

TYPE LOCALITY: Serra da Caraça, Minas Geraës, Brazil.
ILLUSTRATIONS: St. Hil. Hist. Pl. Brés. **1**: *pl. 30. f. 1-4*. 1824.
DISTRIBUTION: Known only from the type locality.
BRAZIL: Minas Geraës: Serra da Caraça, *Saint Hilaire* (P, type of *L. corymbosa*).

The much reduced inflorescence of *L. corymbosa* readily separates it from the other species of the genus. Its sepals are equal in length to those of any species of the genus known from flowering material while its petals are longer. In other respects, particularly in the structure of the leaf-blades, it is obviously related to *L. octandra*, *L. elegans*, and *L. nobilis*.

10. LUXEMBURGIA POLYANDRA St. Hil. Mem. Mus. Paris **9**: 352. 1822.
Luxemburgia polyandra St. Hil. ex Engler in Mart. Fl. Bras. **12**(2): 248. 1876. St. Hil. ex van Tieghem, Ann. Sci. Nat. VIII. **19**: 22. 1904.
Hilairella polyandra (St. Hil.) van Tieghem, Ann. Sci. Nat. VIII. **19**: 24. 1904.
Hilairella neglecta van Tieghem, Ann. Sci. Nat. VIII. **19**: 24. 1904.
Luxemburgia neglecta (van Tieghem) Beauverd, Bull. Soc. Bot. Genève II, **7**: 250. 1915.

Shrubs up to 5 m. high; lenticels numerous, less than 1 mm. long; petioles up to 2.5 cm. long, 0.12–0.2 cm. wide; leaf-blades elliptic, 4–8 cm. long, 1–1.9 cm. wide, triangular or vaguely obtuse at apex,

the terminal cilium up to 6 mm. long, cunéate at base, the marginal teeth appressed-uncinate and frequently replaced by 2–5 pairs of cilia at base, the cilia up to 2 mm. long, the costa prominent above and below, the secondary veins prominulous above and below, 1.5–2 mm. apart, parallel-ascending at about 60° angle; stipules linear-subulate, up to 6 mm. long, the cilia ascending, up to 1 mm. long, 0.5–1 mm. apart; inflorescence racemose, the rachis angular, 10–14 cm. long, the flowers numerous, the bracts deciduous, the pedicels 1–2.5 cm. long, the articulation-stalks scarcely measureable; flower-buds ovate-oblong, up to 8 mm. long, up to 6.5 mm. wide; sepals unequal, imbricate below middle, reflexed above middle, ovate or oblong, 3–4.5 mm. long, 1.7–1.9 mm. wide, acute or obtuse at apex, often apiculate, obtuse at base, the margin entire or irregular; petals subequal, obovate-oblong, 9–10 mm. long, 4–5 mm. wide, obtuse, often retuse or terminating in a distinct gland; stamens about 20, the anthers 5 mm. long, the filaments free, about 1 mm. long; ovaries linear-elliptic or ovate-oblong, about 6 mm. long, the style about 2.5 mm. long; capsule turgid, subterete in cross-section, narrow-oblong, up to 1.6 cm. long, 0.4 cm. wide, the wing subplane or distinctly concave, rounded at apex, 1–1.5 mm. long.

TYPE LOCALITY: Nossa Sehorada Penha, Minas Geraës, Brazil.

ILLUSTRATION: Baillon, Hist. Pl. **4** :361–362. 1873. Beauverd, Bull. Soc. Bot. Genève II. **7**: 238, *pl. 1, f. 5*, leaf, 1915.

DISTRIBUTION: Apparently confined to the mountains of Minas Geraës, Brazil.

BRAZIL: Without locality, *Riedel* s. no. (F, photo and frag., G); Minas Geraës: Villa do Fanado, *Saint Hilaire* s. no. (F, photo and frag. of type collection of *Hilairella neglecta*, G, photo) Minas Novas, *Saint Hilaire* s. no. (F, photo and frag. of type collection of *L. polyandra*, G, photo, K, type collection ? of *L. polyandra*); Olaria, Diamantina, *Mexia 5795* (F, G, NY, US).

Because an adequate description of *L. polyandra* has not been made up to the present time the author deems it necessary to emend all previous descriptions of this species. In his opinion *L. neglecta* cannot be segregated from *L. polyandra*.

The history of *L. polyandra* has been intricate. St. Hilaire in 1822, in a footnote to his original description of *L. polyandra*, promised to describe the species more fully. This he failed to do. An elaborate description was finally published in 1904 by van Tieghem. He founded a new and apparently unwarranted genus, *Hilairella*, with two species. One, *Hilairella polyandra*, he based on part of the unnumbered Saint Hilaire material which the latter had obviously used in describing the original *L. polyandra;* the other, *Hilairella neglecta*, he based on the unnumbered material collected by Saint Hilaire at Villa do Fanado, Minas Geraës, Brazil. Engler, too, obviously used St. Hilaire's material in his earlier description of *L. polyandra*. Although Engler was the first to describe *L. polyandra* at length, his description is incomplete since he based it on part of the material which St. Hilaire had seen but did not adequately describe in 1822. I believe that the segregation of *L. neglecta* is untenable since in the specimens examined, ciliation of the leaf-blades and comparative leaf sizes do not appear to be sufficiently stable characters. Leaf-blades from several parts of the same specimens (*Mexia 5795* and *Riedel* s. no. (G)) reveal that cilia may be present along the basal margin or entirely absent.

The common name of *L. polyandra*, according to Saint Hilaire, is "Congonha do campo."

11. LUXEMBURGIA DAMAZAIOANA Beauverd, Bull. Soc. Bot. Genève II. **7**: 247. 1915.

Luxemburgia Senaei Gilg. in E. and P. Nat. Pfl. 2. **21**: 86. 1925.

Shrubs; leaf-scars about 2 mm. wide; petioles slender, up to 3.5 cm. long; leaf-blades well-spaced, narrow-oblong, 2.5–11.5 cm. long, 0.5–1.5 cm. wide, acute and subtriangular at apex, cuneate (often unequal) at base, the marginal cilia long, stiff, oblique-ascending, up to 4.7 mm. long, rarely paired, the terminal cilium up to 12 mm. long; inflorescence racemose, the rachis scarcely exceeding uppermost leaf-blades in length, smooth or striate, angular, the flowers numerous, the bibracts deciduous, striate, linear-lanceolate, up to 8 mm. long, the pedicels slender, 1.8–2.3 cm. long, the articulation-joint 1–4 mm. from base; buds ovate-oblong, up to 13 mm. long, 6.5 mm. wide; sepals unequal, ovate-rotund or oblong, 6–9 mm. long, 3–6 mm. wide, acute or obtuse at apex, terminating in a cilium 0.5–2 mm. long, the margin entire or minutely irregular with a few elongate cilia clustered at apex; petals subequal, rhomboid to obovate-rotund, 14–17 mm. wide, often retuse at apex, the margin erose; stamens about 17, the anthers 6–9 mm. long, the filaments apparently separate, about 0.4 mm. long; carpels 3-angled, narrow-oblong, 6–8 mm. long, the style about 1.5 mm. long; capsule subterete in cross-section, oblong-rectangular, 1–1.5 cm. long, about 0.4 cm. wide (before dehiscence), the mature seeds terete, about 1.2 mm. long, the wing absent or not exceeding 0.2 mm. in length (Fig. 1, *a—j*).

TYPE LOCALITY: Santa Luzia, Serra do Cipó, Minas Geraës, Brazil.

ILLUSTRATION: Beauverd, Bull. Soc. Bot. Genève II. **7**: *pl. 3, f. 1–10.* 1915.

DISTRIBUTION: Apparently known only from the type locality.

BRAZIL: Minas Geraës: Santa Luzia, Serra do Cipó, *Damazio 2071* (F, frag. of type of *L. Damazioana*); *Mello* and *Brade 1235* (F); *Samp.* and *Mello 6899* (F); *Mello 6150, 6151* (F); *Schwacke 10758* (F, photo of type of *L. Senaei*).

L. Damazioana is distinguished from *L. Gardneri* by its narrower leaf-blades which lack uncinate teeth on the margin. As in *L. polyandra*, the articulation-stalk of the pedicels of *L. Damazioana* is scarcely measureable, the sepals are long-ciliate at the apex, the petals are larger, and the style is obviously shorter. *L. polyandra* shows additional differentiating characters in having the margins of the leaf-blades with simple uncinate teeth above the base, the leaf-blades with a short terminal cilium at the apex, the sepals reflexed, the petals narrower, the stamens fewer, and the styles shorter.

12. LUXEMBURGIA MAJOR (van Tieghem) Beauverd, Bull. Soc. Bot. Genève II. **7**: 246. 1915.

Epiblepharis major van Tieghem, Jour. de Bot. **15**: 393. 1901.

Shrubs; branchlets lenticellate; leaf-scars rotund or compressed-rotund, about 3 mm. wide; petioles slender, 2–3 cm. long, 0.1 cm. wide, ascending, 2–4 mm. apart, the leaf-blades oblong, 6–13 cm. long, 2–3 cm.

wide, triangular or subrotund at apex, the terminal cilia 5–9 mm. long, narrow-cuneate at base, the costa prominent beneath, the marginal teeth uncinate, each tooth with a cilium up to 3 mm. long arising from upper surface of lamina (at base of tooth) and terminating an irregular tertiary vein the secondary veins prominulous above and below, about 2–3 mm. apart in middle; stipules linear-subulate, up to 1 cm. long, the cilia short, parallel and oblique-ascending; inflorescence, flowers, and fruit not seen.

TYPE LOCALITY: Petropolis, Rio de Janeiro, Brazil.
ILLUSTRATION: van Tieghem, Jour. Bot. **15:** 393, *f. 4.*, leaf of *Epiblepharis major*, 1901.
DISTRIBUTION: Known only from the type locality.

BRAZIL: Rio de Janeiro: Petropolis, *Glaziou 8618* (F, photo, P, veg. parts of type collection of *L. major*).

I have chosen to retain this species as separate from *L. Gardneri*. Its longer leaf-blades, shorter petioles, basally unequal lamina, and subvillose stipules seem to warrant this segregation. In order to evaluate better the species flowering material will be necessary.

13. LUXEMBURGIA GLAZOVIANA (Engler) Beauverd, Bull. Soc. Bot. Genève II. **7:** 246. 1915.

Luxemburgia polyandra St. Hil. ex Engler var. *Glazoviana* Eichl. in Mart. Fl. Bras. **12**(2): 358. 1876.
Epiblepharis Glazoviana (Engler) van Tieghem, Jour. de Bot. **15:** 392. 1901.

Shrubs; lenticels linear, 5–7 mm. long, about 0.3 mm. wide; leaf-scars oblique and prominent; petioles 1.5–2.5 cm. long; leaf-blades narrow-elliptic, 3–8 cm. long, 0.8–2 cm. wide in middle, triangular or round-obtuse at apex, the terminal cilium 6–8 mm. long, cuneate and scarcely unequal at base, the marginal teeth oblique ascending and glandular-black, black and obtuse at apex, each tooth up to 0.5 mm. long, bearing a slender subulate cilium at base, about twice its length, the cilia arising from ventral margin of leaf-blade, the costa prominent above and below, the secondary veins scarcely elevated above and below, 1–3 mm. apart; stipules deciduous, linear-subulate, up to 5 mm. long, the cilia well spaced and angular-ascending; flower-buds ovate-rotund, up to 9 mm. long, 7 mm. wide; inflorescence racemose, the rachis exceeding the uppermost leaf-blades, the pedicels slender, angular, 2.5–3 cm. long, the articulation-joint 1–1.2 cm. from base; sepals 5–7, unequal, elliptic-lanceolate, 5–7.5 mm. long, 2.5–4 mm. wide, acute and often triangular-acuminate at apex, obtuse at base, terminating in a short blunt cilium about 0.5 mm. long, the margin entire or minutely erose; petals 5–8 subequal, rotund to obovate-rotund, about 10 mm. long, 8–10.5 mm. wide, rounded, retuse or bilobed at apex, scarcely tapering toward base; stamens 20–40, the anthers up to 6.5 mm. long; pistils 6–7 mm. long; pistils 6–7 mm. long, the ovary about 1.6 wide in cross-section, the style about half length of ovary; capsule oblong, 1.5 cm. long, about 0.5 cm. wide, the seeds roughly triangular in cross-section, up to 1.5 mm. long, often with a distinct terminal wing, the latter concave, up to 0.1 mm. beyond body of seed, and extending laterally along margin of seed.

TYPE LOCALITY: Palatinato, Rio de Janeiro, Brazil.
ILLUSTRATION: van Tieghem, Jour. de Bot. **15:** 392. *pl. 3*, 1901.
DISTRIBUTION: Known only from the State of Rio de Janeiro, Brazil.

BRAZIL: Rio de Janeiro: *Glaziou 8615* (F, frag.); Neachi de Nova, Friburgo, *Glaziou 2709* (P, cotype of *L. polyandra* var *Glazoviana*).

14. **Luxemburgia villosa,** sp. nov.

Suffrutices scandentes; petiolis gracilibus, 2–3.5 cm. longis; laminis foliorum ascendentibus vel paullum laxis angusto- vel lato-oblongis, 3.5–5 cm. longis, 0.7–2.5 cm. latis, apice acutis vel triangularibus cilio terminale, 5–7 mm. longo, basi lato-cuneatis vel obtusis marginibus uncinato-dentatis ciliis obliquo-ascendentibus, 1–2 mm. distantibus, subulatis, 2–3 mm. longis, ad basim extendentibus costa supra prominente et subtus plana venis secundariis subplanis, in medio 1.5–2 mm. distantibus; stipulis inter superiora folia persistentibus aut deciduis linearibus, ad 7 mm. longis, ciliis crebris villosis dendriticisque basi ramulis brevioribus; gemmis angusto-oblongis, circiter 1 cm. longis, 0.5 cm. latis; inflorescentiae racemosae floribus multis rhachidibus striatis angularibus superiora folia non excedentibus, bracteis stipuleanis, pedicellis gracilibus, ad 2.5 cm. longis, circiter 0.6 mm. latis, a basi loco articulationis ad 3 mm. longo locato; sepalis evidenter inaequalibus infra medium imbricatis ovato-oblongis, 3.5–5 mm. longis, apice in gracilem longo-ciliatum acumen attenuatis, ciliis infra medium ad 2 mm. longis, interioribus oblongis, 5–8.5 mm. longis, apice acutis longo-apiculatisque apiculo recto, 1–1.5 mm. longo, marginibus scariosis minuto-irregularibus ad apicem rare breve ciliatis; petalis inaequalibus (hic gemmis) obovatis, ad 11 mm. longis; stâminibus circiter 25 antheris linearibus, circiter 6.5 mm. longis, filamentis circiter 0.5 mm. longis, pistillis ad 6 mm. longis, ovariis oblongis; fructibus non visis.

TYPE LOCALITY: Serra do Cipó, Minas Geraës, Brazil.
DISTRIBUTION: Known only from the type locality.

BRAZIL: Minas Geraës: Serra do Cipó, *Lund* (*Glaziou* ?) *884 a* (P, type of *L. villosa*).

The type collection bears two labels, one written in hand naming Lund as the collector and bearing a pencilled number *884a*, the other with Glaziou's name in print and lacking a collection number. On the Lund label the plant is described as climbing in habit. If *L. villosa* be so, it is the only species of the genus known to possess this character.

The villose nature of the stipules (from which the species derives its name), as well as the general structure of the leaves indicate *L. villosa* is related to *L. Gardneri*. On the basis of floral structure, as ascertained by dissection of the buds, it appears to be closely related to *L. Glazoviana* and *L. Gardneri*. Its ovate-oblong sepals exhibit a slightly irregular margin and a conspicuous apiculum (1–1.5 mm. long) in contrast to the regular margins of the sepals and the short blunt apical cilium and glandular knob of the sepals of these respective species. Its petals are more obovate than the petals of *L. Glazoviana* and *L. Gardneri* which are obovate-rotund in character. The fact that the sepals and petals of *L. villosa* and *L. Gardneri* appear to be pentamerous while those of *L. Glazoviana* vary from 5–8 in number

may indicate a closer relationship between the first two species. In studying the six species constituting the Petiolatae Section of the genus one encounters difficulty in establishing interspecific relationships on the basis of floral characters because of the lack of flowering material in two of the species: *L. major* and *L. diciliata*.

15. LUXEMBURGIA GARDNERI (van Tieghem) Beauverd, Bull. Soc. Bot. Genève II. **7**: 245. 1915.

Luxemburgia ciliosa (Mart.) Planch. in Hook. Ic. 6. **1**: *pl.* 516. 1843, not *Plectanthera ciliosa* Martius, Nov. Gen. **1**: 40. 1824.
Epiblepharis Gardneri van Tieghem, Jour. de Bot. **15**: 390. 1901.

Shrubs; petioles about 3.5 cm. long; leaf-blades widely or narrow-elliptic, up to 9 cm. long, 0.9–2.7 cm. wide, acute at apex with long terminal cilium up to 8 mm. long, subcuneate at base (rarely unequal), the marginal teeth obtuse-capitate, 0.8–3 mm. apart, the cilia linear-subulate, at least twice length of teeth, a single cilium arising from upper basal angle of each tooth, the costa prominent above and below, the secondary veins scarcely prominent; stipules linear, up to 8 mm. long, the cilia subvillose; inflorescence short-umbelliform-racemose, scarcely exceeding uppermost leaf-blades (or up to 8 cm. beyond uppermost leaf-blades), the pedicels of flowers up to 4.5 cm. long, the articulation-stalks up to 1.5 cm. long; flower-buds ovate-oblong, about 1 cm. long, 0.5 cm. wide; sepals imbricate at anthesis, unequal, oblong, 5–11 mm. long, 2.3–4 mm. wide, acute and rostrate at apex, terminating in glandular knob, the margin entire; petals almost equal, obovate-rotund, up to 11 mm. long, 9 mm. wide; stamens about 30, the anthers up to 5.5 mm. long; carpels often smooth, oblong, up to 5 mm. long, about 2 mm. wide, the style usually more than half length of ovary; capsule oblong-rectangular, 1.2–1.6 cm. long, 0.6–0.75 cm. wide, 3-angled in transverse section, the seeds oblong, 0.3 mm. long, 0.5 mm. wide, the wings auriculiform, somewhat concave, extending about 0.5 from seed, narrow laterally and basally.

TYPE LOCALITY: Diamantina, Minas Geraës, Brazil.
ILLUSTRATION: van Tieghem, Jour. de Bot. **15**: *pl. 2*. 1901. Hook. Ic. 6. **1**: *pl. 516*. 1843.
DISTRIBUTION: Known from the State of Rio de Janeiro, and Minas Geraës, Brazil.

BRAZIL: Rio de Janeiro: Serra dos Orgaos, 1500 m. alt., *Gardner 5677* (F, K, NY type collection of *L. Gardneri*); without locality, *Guillemin 855* (F); Petropolis au Morin, *Glaziou 12531* (F, photo and frag., K, P).

To van Tieghem belongs the distinction of noting the differences between the plant collected and described by Martius as *Plectanthera ciliosa*, and *Gardner 5677*, which Planchon thought to be conspecific when he transferred the Martius species to the genus *Luxemburgia*. Engler (5) also accepted these collections as representing one species. Van Tieghem (9), however, noted (and illustrated) that the leaf-blades of the Martius specimen, which unfortunately I have not seen, had essentially entire and ciliate margins, while those of *Gardner 5677* were falcate-serrate with a cilium at the base of each tooth this appears; to arise from the upper surface of the lamina. On the basis of these characters he segregated *Gardner 5677* as *Epiblepharis Gardneri*, making it the type of the new genus. Beauverd (2) however, later transferred

E. Gardneri to the genus *Luxemburgia* and cited *Glaziou 12531* as conspecific.

It is evident that Planchon and Engler, although having seen the Martius material, used other specimens for their plates. These plates seem to match well the Gardner and Glaziou collections of *L. Gardneri*.

The fact that Engler in his description of *L. ciliosa* notes that the three outer sepals are ciliate on the margins (a character which he uses to differentiate this species as *L. polyandra*), makes it probable that the Martius collection has sepals of this kind. Critical examination of the buds of two collections of *L. Gardneri* (*Gardner 5677* and *Glaziou 12531*), however, reveals that the sepals are without marginal cilia.

16. **Luxemburgia diciliata,** sp. nov.

Suffrutices; cicatricibus foliorum evanescentibus, 1.5–2.3 mm. latis; petiolis 0.5–0.75 mm. latis, laminis foliorum apicibus ramulorum crebris anguste lineare-obovatis vel angusto-ellipticis, 4.5–6 longis, 1.5–1.7 cm. latis, apice vel subrotundis attenuatis cilio 3.5–8 mm. longo, basi cuneatis, marginibus subvillosis dentibus falcatis, circiter 1 mm. longis, dente utroque duobus ciliis vix obliquis, 4.2–6.5 mm. longis, alio ascendente et ventrale (angulo cilii laminaeque), alio dorsaliter basaliterque disposito, laxe in petiolum decurrentibus (ad 2–6 mm.), costa utrimque prominente, venis secundariis circiter 35, parallelis obliquo-ascendentibus stipulis linearibus, 5.5–7.5 mm. longis, basi circiter 3 mm. latis, ciliis longis tortisque; floribus fructibusque non visis.

TYPE LOCALITY: Prov. Bahia, Brazil.

DISTRIBUTION: Known only from the type collection.

BRAZIL: Bahia: *Luetzelburg 238* (NY, type of *L. diciliata*).

Although this species has been described from sterile material, the conspicuous paired cilia of the leaf margins distinguish it from the rest of the genus. From this character the species derives its name.

The Province of Bahia where the type collection was made, represents the most northern limit of the entire genus.

The structure of the stipules of *L. diciliata* seem to point to the fact that this species is more closely related to *L. Gardneri* than to *L. Glazoviana*.

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Studies in the Araceae—I

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1. A New Anthurium from Ecuador

Anthurium Espinosanum sp. nov. (Sect. *Digitinervium* Sodiro) fig. 1.

Herba epiphytica, erecta, parva, scandens; caudex erectus vel arcuatus; folia erecta, persistentia; petiolus glaber, ad basim expansus; lamina undulata, nervosa, ovato-elliptica, acuta, ad basim leviter acuminata; nervi prominentes, ad marginem confluentes; inflorescentia erecta, parva, viridis; spatha ovato-lanceolata, acuta vel leviter obtusa, ad basim leviter undulata; spadix erectus, viridis, cylindricus, ad apicem obtusus et attenuatus, ad basim nudus; flores quadrangulares, irregulares.

Climbing, erect epiphyte of small stature. Stem straight or slightly curved, 10–17 cm. long, ca. 1 cm. in diameter, producing numerous flat grey roots and several leaves at or near the summit, mostly covered by remnants of sheaths, leaf-bases, and roots; sheaths brown, vaguely ovate in outline, acutish, rapidly deteriorating into a complex webbed series of fibers. Leaves several, often persistent half-way down the stem, long-petioled, mostly erect; petioles glabrous, abruptly enlarged at base, to 10 cm. long, ca. 2 mm. in diameter, with a slight pulvinus at leaf-base; blades very undulate when dry, prominently nervose, thin, dark green above, whitish-green below (fide coll.), ovate-elliptic, acute, somewhat acuminate basally, 11–12.5 cm. long, 7–8 cm. across; nerves prominent on both surfaces, more so below, the median raised above and below, extending to tip, the secondaries usually 11, somewhat ascending, confluent into a peripheral vein which runs about 2–3 cm. inside the margin and extends to the margin at apex of blade. Inflorescences erect, small, produced from apex of stem or some distance down it, 10.5–15.5 cm. long when measured from tip of spadix. Spathe at right angles to spadix, reddish-green (fide coll.), ovate-lanceolate, acute to somewhat obtuse, ca. 2 cm. long, 3 mm. broad at base, where it is slightly undulate. Spadix stiffly erect, green (fide coll.), cylindrical, obtuse and narrowing somewhat at apex, ca. 3.5 cm. long, 2.5–3 mm. in diameter, with a naked area about 1 mm. long at base. Flowers rather elongately and irregularly quadrate.

Type: *Reinaldo Espinosa 1177*, collected at Torata (road to Santa Rosa), Provincia de Loja, Ecuador, on 26 December 1946. The collector's notes are as follows: "Epífita. Hojas ovaladas agudas, verde oscuro en el haz, brilliantes; blanquecinas en el envés. Bráctea y tallo floral con tinte rojizo. Espiga verde. Unos 60 á 80 m."

This unusual little species, with a foliar shape not often encountered in the genus *Anthurium*, is dedicated to the late Dr. Reinaldo Espinosa, of the Universidad de Loja, collector of the excellent type material. It is probably best placed in the section *Digitinervium* Sodiro, though it is not related to any species of that group with which we are familiar.

2. A New Section of Amorphophallus Blume

Amorphophallus Blume, sect. **Exesispadix** sect. nov.

Herbae robustae; folia trisecta, segmentis membranaceis; spatha magna, coriacea, ovata; spadix erectus, magnus, ad apiceum foliosus exesus et incrassatus, ad basim cylindricus.

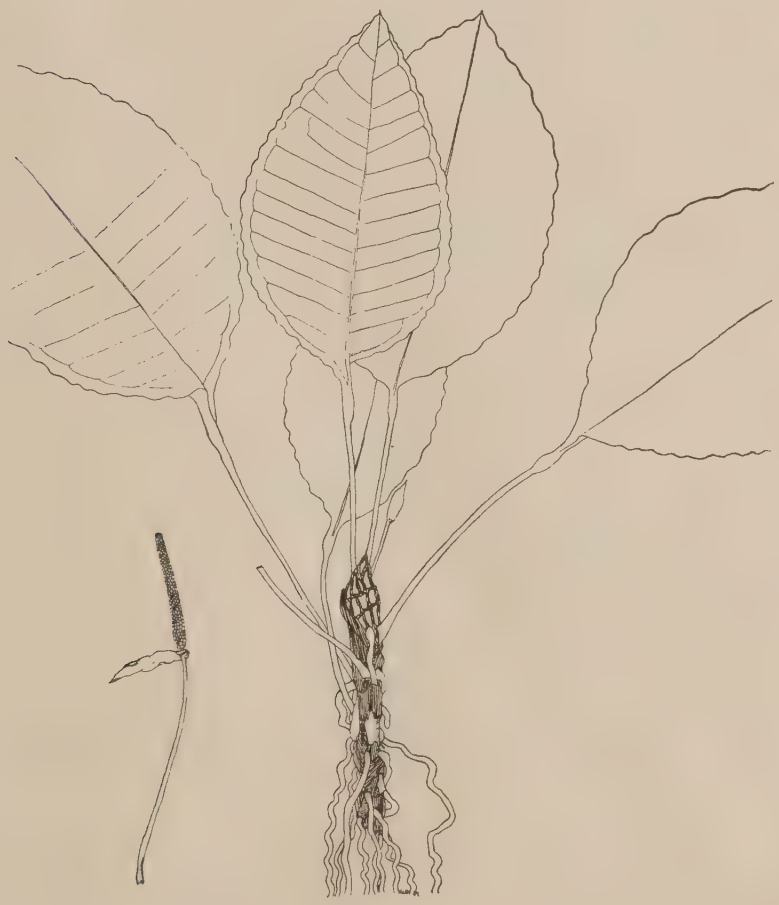

FIG. 1. *Anthurium espinosanum*, n. spec.

The new section is most closely allied to section *Conophallus* (Schott emend.) Engler, through the East African *Amorphophallus maximus* (Engler) N. E. Brown. The single species thus far detected may be diagnosed as follows:

Amorphophallus congoensis sp. nov. (Sect. *Exesispadix* A. D. Hawkes).

Herba terrestris, robusta; folia trisecta, segmentis membranaceis, oblanceolatis usque ad elliptico-lanceolatis, longe-acuminatus; spatha viridis et purpurea, maculata, magna, coriacea, ad apicem undulata, obtusa vel truncata, ovata. Spadix erectus, magnus, ad apicem foliosus exesus et incrassatus, oblanceolatus, acuminatus, purpureus, ad basim cylindricus; flores numerosi.

Gigantic erect terrestrial herb, "total height about 8 ft.," (fide coll.). Stem "1½ inches in thickness near base, light green with elongate spots of dark green or dark purplish." Leaves expanding "when the flower is fully developed," trisect, the segments ca. 19–40 cm. long, 9–15 cm. wide when expanded; pinnae 6–12, from a more or less flattened rachis which becomes winged and ca. 1 cm. wide toward the apex, membranaceous, lighter green below, with rather prominent ascending veins on the upper surface, oblanceolate to elliptic-lanceolate, long-acuminate, 6.5–13.5 cm. long, 2.5–4 cm. wide. Peduncle erect, evidently somewhat flattened, striate, ca. 22 cm. long and 1.5 cm. wide when dried. Spathe "green on outer surface, spotted with dusky green, and shading to purplish near upper edge; inside dark purplish, except for a zone of light green opposite upper limit of pistillate flowers," with a basal area of rough brownish papillae, ca. 36 cm. long and ca. 22.5 cm. wide (incomplete in our specimen), rather fleshy, undulate and folded toward apex, where it is obtuse or truncate, vaguely ovate in over-all outline. Spadix incomplete in our specimen, evidently ca. 22 cm. long, foliose and hollow above, where it becomes 10 cm. wide, then narrows to a folded, probably acuminate point; oblanceolate, "dull purple," bearing flowers on cylindrical base, which is only about 2.25 cm. wide; flower-bearing area ca. 10–11 cm. long. Flowers very numerous, the pistillate at base, scattered, "light green, stigmas now blackish," ca. 1 mm. high and 2 mm. in diameter, urceolate, with flaring twin-lobed stigma at apex; staminate flowers very numerous, separated from pistillate by irregular naked area, "dull purple," tightly clustered, 1 mm. high and broad, usually two together.

TYPE: *J. P. Chapin 615*, collected at Lukolela, Congo River, Belgian Congo, on 6 November 1930. The collector's notes state: "Large Jack-in-pulpit. Taken when 1 ft. above ground and 1½ in. thick." The type specimens are preserved in the herbarium of The New York Botanical Garden.

Amorphophallus congoensis is a large and spectacular species which has apparently escaped prior detection by students of this fascinating paleotropical genus. It is evidently not closely allied to any previously described species.

Taxonomic Notes on the Ustilaginales

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From the autumn of 1947 to the spring of 1951, the writer enjoyed the privilege of studying the excellent collection of smut fungi in the Mycological Collections of the Bureau of Plant Industry at Beltsville, Maryland. Visits to other herbaria in this country and in Europe have given him additional opportunities of examining many other collections of this group of fungi. As a result many critical taxonomic notes as well as numerous unrecorded extensions of geographic and host ranges for many species have been accumulated. A part of this material is presented in the present paper.

The writer is deeply indebted to John A. Stevenson for his constant interest and his valuable assistance in various ways. He also wishes to express his thanks to Edith K. Cash for preparing the Latin diagnoses and for a review of the manuscript; to Mrs. Agnes Chase for the identification of certain grass hosts; and to the curators of various herbaria mentioned in this paper for the privilege of examining material under their care.

Herbaria where the specimens cited are located are referred to according to the following abbreviations: BPI = Mycological Collections, Bureau of Plant Industry, U. S. Department of Agriculture; BR = Jardin Botanique de l'Etat, Brussels; CH = Clinton Herbarium, Connecticut Agricultural Experiment Station; CMI = Commonwealth Mycological Institute, Kew; FH = Farlow Herbarium, Harvard University; NY = New York Botanical Garden; PRM = Mycological Herbarium, Union Department of Agriculture, Pretoria; S = Naturhistoriska Riksmuseet, Stockholm; US = U. S. National Museum.

Tilletia hyalospora Mass. Kew Bull. 153–154: 148. 1899.

Tilletia boliviensis Liro Ann. Bot. Soc. Zool.-Bot. Fenn. Vanamo **6**: 1. 1935.

On *Nassella pubiflora* (Tr. & Rupr.) Desv., near Sorata, Bolivia, in G. Mandon, Plantae Andium Boliv. 1275, type (NY, S); La Paz, Bolivia, Mar. 20, 1920, E. W. D. & Mary M. Holway 430 (US 1108465); Tequina, Cochabamba, Bolivia, Jan. 6, 1924, A. S. Hitchcock 22857 (US 1163907).

On *Nassella* sp., Ccatcca, prov. Quispicanchis, Dept. Cuzco, Peru, Mar. 1938, C. Vargas, sub *Tilletia oryzopsidis* Zundel (BPI).

The type collection of *Tilletia hyalospora* is also the cotype of *Tilletia boliviensis*. The host was incorrectly given by Massee as *Piptochaetium*.

Tilletia zundelii Hirschh. Rev. Argent. Agron. **10**: 187. 1943.

On *Setaria* sp., East Palm Beach, Florida, United States, Oct. 1, 1919, without collector (BPI).

Urocystis oxalidis Pazschke Hedwigia **31**: 94. 1892.

On *Oxalis tuberosa* Molina, Yanyos, 2,800 m., Dept. Lima, Peru, comm. C. Bazan de Segura, Dec. 1949 (BPI).

USTILAGO LONGISSIMA (Sow. ex Schlecht.) Meyen Pflanzen-Path. 124. 1841.

Ustilago underwoodii Zundel Mycologia **34**: 124. 1942.
Entyloma peninsulae Crowell Canad. Jour. Res. C. **20**: 328. 1942.

On *Panicum virgatum* L. Staten Island, New York, United States, Sep. 19, 1939, L. A. Kolk (BPI).

On *Zizania aquatica* L., New Glasgow, N. S., Canada, Aug. 20, 1906, W. P. Fraser, type of *E. peninsulae* (BPI).

Although this species is usually considered as occurring only on species of *Glyceria*, the two collections cited above differ from the *glyceria* form neither microscopically nor macroscopically. Both have light olivaceous spores measuring 4.5–7.5 μ in diameter.

USTILAGO PANICI-PROLIFERI P. Henn. Bot. Gaz. **28**: 274. 1899.

Sori surrounding the axes of young panicles, inhibiting entirely the development of inflorescences, elongate-obclavate, tapering toward the apices, 2.5–7 cm. long, partially concealed by leaf sheaths, each covered by a papery, transparent membrane of host tissue which ruptures irregularly exposing a dusty, dark spore-mass. Spores olive brown, globose to ellipsoid, 7–10.5 x 6.7–9 μ, occasionally more elongate and irregular, up to 14 μ in length; epispore approximately 1 μ thick, smooth.

On *Panicum dichotomiflorum* Michx. (= *P. proliferum* Lam. var. *acuminatum* Michx.), prov. Urbena, Mexico, in Syd. Ustil. 212, type (BPI).

On *Panicum paludivagum* Hitch. & Chase, Miquelete, Dept. de Montevideo, Uruguay, in Syd. Fungi Exot. Exs. 937, sub *Ustilago paspali* (BPI); Miquelete, Uruguay, in Herter, Plant. Urug. 802b (FH).

The last collection cited above was reported by Ciferri and Herter (1) as *Ustilago argentina* Speg.

USTILAGO SCHROETERIANA P. Henn. Hedwigia *35*: 215. 1896.

Tilletia paspali Zundel Mycologia **23**: 299. 1931.

On *Paspalum millegranum* Schrad., Matta de Sao Joas, Bahia, Brazil, Jan. 3, 1925, A. Chase 8140½, type of *T. paspali* (BPI).

On *Paspalum* sp., St. Catharina, Brazil, Nov. 1885, E. Ule 1615, type, (CH); Turrialba, Costa Rica, Mar. 27, 1948, C. E. Chardon (BPI).

Unless the type of *Tilletia paspali* is a mixed collection, the spore size given in its original description is much too large.

USTILAGO VESICULOSA P. Henn. Hedwigia *35*: 51. 1896.

Sphacelotheca echinata Zundel Mycologia **23**: 298. 1931.
Crozalsiella argentina Hirschh. Not. Mus. La Plata **5**: 236. 1940.

Sori destroying the young panicles, transforming each into a subglobose to oval, dark, dusty spore-mass, 3–6.5 mm. diam., enclosed in a persistent, thick, green membrane of host tissue which tapers at the apex into a slender, elongate, spire-like structure. Spores ochraceous to reddish brown, subglobose, ovoid, or broadly ellipsoid, finely but densely echinulate, often even appearing as semi-reticulate, 8.5–12 μ in length, endospore often vacuolate; sterile cells about the size of spores, scattered throughout the sorus.

On *Panicum demissum* Trin., Campo Bello, Brazil, Feb. 1894, E. Ule 2080, cotype (CH); Estado de Rio Janeiro, Brazil, in E. Ule, Herb. Brazil, 2083 (FH); Serra Geral, Brazil, in Rab.-Wint. Paz., Fungi Eur. 4008 (BPI); Serra do Caparao, Brazil, Apr. 30-May 4, 1925, A. Chase 9731½, cotype of *S. echinata* (BPI); El Prado, Park of Montevideo, Uruguay, Oct. 22, 1905, R. Thaxter 7908 (FH).

Ustilago alismatis sp. nov.

Soris in foliis petiolisque solitariis, ellipticalibus vel elongatis, minutis, usque 1.5 mm. longis, contextu infecto hospitis demum perforato; sporis globosis vel ovoideis, 28.5–36 μ in diam. vel 27–39 x 21.–31.5 μ; episporis aureo-flavidis, glabris, 2–3 μ crassis.

Sori in the leaves and petioles, isolated, elliptical to elongate, up to 1.5 mm. long, the infected tissues becoming perforated eventually. Spores globose to oval, 28.5–36 μ in diam., or 27–39 x 21–31.5 μ; epispore golden yellow, smooth, 2–3 μ thick.

On *Alisma plantago-aquatica* L., Provo, Utah, United States, June 23, 1926, A. O. Garrett, type (BPI).

Ustilago eriochloae sp. nov.

Soris inflorescentiam totam destruentibus, semi-agglutinatis, 5–11 cm. longis, axem rhachidesque inflorescentiae circumdantibus, spiculis rudimentariis interdum ad pedicellos affixis restantibus; sporis globosis usque ovalibus, 13.5–18 x 12.5–15 μ, episporis olivaceo-brunneis, subtiliter sed dense echinulatis, circa 1 μ crassis.

Sori destroying the entire inflorescence, semi-agglutinate, 5–11 cm. long, surrounding the axis and rachides of the inflorescence, sometimes with rudimentary spikelets remaining attached to the pedicels. Spores globose to oval, 13.5–18 x 12.5–15 μ; epispore olivaceous brown, finely but densely echinulate, about 1 μ thick.

On *Eriochloa punctata* (L.) Desv., Turrialba, Costa Rica, Sept. 29, 1947, F. L. Wellman, type (BPI).

This species probably belongs to the genus *Sphacelotheca* and the failure to detect a false membrane is possibly due to its early disintegration in the mature sori such as are found in the present collection.

SPHACELOTHECA CORDOBENSIS (Speg.) Jacks. Jour. Dept. Agr. Porto Rico **14**: 298. 1930.

Sphacelotheca viegasiana Zundel Mycologia **31**: 588. 1939.

On *Trichachne sacchariflora* (Raddi) Nees, Terreno baldio, Campinas, Est. S. Paulo, Brazil, Oct. 5, 1935, A. P. Viegas 2554, type of *S. viegasiana* (BPI).

SPHACELOTHECA MILDBRAEDII (H. & P. Syd.) Zundel Mycologia **22**: 135. 1930.

Ustilago mildbraedii H. & P. Syd. Wissensch. Ergebn. Deutsch. Zentr.-Afr. Exped. 1907–1908. II. **2**: 95. 1911.

Sori in the inflorescences, each involving a pair of racemes, entirely concealed by the enveloping spathe at earlier stages, fusiform, 7–15 mm. long, 1.5–3 mm. diam., enclosed in a thin, grayish false membrane which decomposes early into its component sterile cells scattered throughout

the sorus; sterile cells light yellow, frequently deeply compressed so as to appear as stellate from above, 8.5–13.5 x 7–12 μ. Spore-mass dusty, dark, surrounding a remnant peduncle with paired rachides at the tip and often even with rudimentary pedicels attached. Spores spherical to subspherical, occasionally oval, reddish brown, 4.5–7 x 4.5–6 μ; epispore 0.5 μ thick, finely but distinctly echinulate.

On *Cymbopogon afronardus* Stapf, Kawanda, Uganda, July 1940, C. G. Hansford (BPI); Kakitumbe-Bach, Mpororo, Tanganyika, July 23, 1907, J. Mildbraed 357, type (CH, S).

The host of the type collection was originally recorded as *Cymbopogon schoenanthus* (L.) Spreng.

SPHACELOTHECA TRACHYPOGONIS Zundel Mycologia **25:** 353. 1933.

On *Trachypogon montufari* (H. B. K.) Nees, Brazil, intercepted at the Plant Quarantine Inspection House, Washington, D.C., United States, April 13, 1948 (BPI)

Sphacelotheca vanderysti (P. Henn.) comb. nov. (Fig. 1, A)

Ustilago vanderysti P. Henn. Ann. Mus. Congo Bot. V. **2:** 86. 1907.
Ustilago hyparrheniae Beeli Bull. Jard. Bot. Bruxelles **8:** 6. 1922.
Cintractia vanderysti Zundel Mycologia **22:** 128. 1930.
Sphacelotheca evansii Zundel Mycologia **22:** 133. 1930.
Sphacelotheca ritchiei Zundel Mycologia **22:** 138. 1930.
Sphacelotheca ruprechtii Syd. Ann. Myc. **33:** 232. 1935.
Sphacelotheca kenyae Zundel Mycologia **29:** 586. 1937.
Ustilago hyparrheniae Hopkins Trans. Rhodesia Sci. Assoc. **35:** 126. 1938.

Sori in the inflorescences, each involving a pair of racemes, usually forked at the upper part to surround the paired rachides, but united at the base around the peduncle, cylindrical, 4–8 mm. in length, partially concealed by the spathe, covered at first by a brownish false membrane which ruptures irregularly disclosing a dark, semi-agglutinate spore mass; sterile cells of the membrane hyaline, thin-walled, globose to ellipsoid, 9–16.5 μ in length. Spores chiefly globose to oval, 7–11 μ diam., often somewhat irregular, the elongate ones up to 12.5 μ in length, yellowish or olivaceous brown, usually more or less smoky tinted; epispore approximately 0.7 μ thick, punctate to finely echinulate under higher magnifications.

On *Hyparrhenia cymbaria* (L.) Stapf, Morogoro, Tanganyika Territory, Jan. 1926, A. H. Ritchie, type of *S. ritchiei* (PRM 20650).

On *Hyparrhenia diplandra* (Hack.) Stapf, Kisantu, Belgian Congo, May 8, 1907, H. Vanderyst 1908 (BR); Kimpese, Belgian Congo, June 1914, H. Vanderyst 4404, type of *U. hyparrheniae* Beeli (BR).

On *Hyparrhenia dissoluta* (Nees) Hubb. (= *H. ruprechtii* Fourn.), Olifants River, Transvaal, South Africa, Apr. 1, 1918, I. B. Pole Evans, type of *S. evansii* (PRM 14174); Marikana, Rustenburg, Transvaal, South Africa, Mar. 10, 1934, type of *S. ruprechtii* (PRM 27377); Barberton, Transvaal, South Africa, Feb. 4, 1911, I. B. Pole Evans, sub *Sphacelotheca andropogonis* (Opiz) Bub. (PRM 1156).

On *Hyparrhenia filipendula* (Hochst.) Stapf, Charter, Southern Rhodesia, Feb. 28, 1933, J. M. Rattray, type of *U. hyparrheniae* Hopkins (BPI); west of Brisbane, Queensland, Australia, Mar. 22, 1943, M. S. Clemens (BPI).

On *Hyparrhenia rufa* (Nees) Stapf, N. Dembo, Belgian Congo, June 1906, H. Vanderyst B31, lectotype (BR 334); Kisantu, Belgian Congo, July 1906, H. Vanderyst B68 (BR 333).

Fig. 1. A. *Sphacelotheca vanderysti* on *Hyparrhenia dissoluta* (PRM 27377). B. *Sorosporium tembuti* on *Hyparrhenia dissoluta* (PRM 9693). x 1.

On *Hyparrhenia* sp., Eldoret, Belgian Congo, May 8, 1929, A. S. Hitchcock 25028, type of *S. kenyae* (BPI).

Hennings (2) enumerated four collections in his original description, which is rather meager to be helpful in delimiting this species. One of

them (Vanderyst B32) is a *Sorosporium* on *Andropogon gabonensis* Stapf and another (Vanderyst B34) is identical with *Sphacelotheca congensis* (Syd.) Wakef. on *Hyparrhenia* sp. The other two collections are cited above as belonging to this species. In order to avoid further confusion, one of these two collections is selected and proposed as the lectotype.

Sorosporium concelatum sp. nov.

Soris in ovariis, spiculas omnes paniculae infectantibus, 2–3 mm. longis, oblongis, utrinque attenuatis, e glumis omnino tectis, soro quoque membrana griseola e textura hospitis mycelio fungoso penetrata composita tecto; glomerulis sporarum opacis, subglobosis usque oblongis vel irregularibus, 30–104 x 27–70 μ; sporis polyedricis, 7–10.5 x 5.5–9.5 μ, peripheris intense cinnamomeo-brunneis, in superficie libera dense verruculosis, interioribus sub-hyalinis usque pallide brunneis, glabris.

Sori in the ovaries, infecting all the spikelets in a panicle, 2–3 mm. long, oblong, tapering at both ends, completely concealed by the glumes, each enclosed in a grayish membrane of host tissue infiltrated by the fungus mycelium. Spore-balls opaque, subglobose to oblong, or irregular, 30–104 x 27–70 μ. Spores polyhedral, 7–10.5 x 5.5–9.5 μ; peripherical spores deep cinnamon brown, densely verruculose on free surface; inner spores subhyaline to light brown, smooth.

On *Arundinella nepalensis* Trin., Gilgandra, New South Wales, Australia, 1928, without collector, type (BPI).

This collection was reported by Zundel (6) as *Sorosporium arundinellae* Syd. which is a synonym of *Ustilaginoidea arundinellae* P. Henn.

SOROSPORIUM ISCHAEMOIDES (P. Henn.) Zundel Mycologia **29**: 587. 1937.

Ustilago ischaemoides P. Henn. Ann. Mus. Congo Bot. V. **2**: 86. 1907.
Sorosporium wildemanianum P. Henn. Ann. Mus. Congo Bot. V. **2**: 87. 1907.
Sorosporium austro-africanum Zundel Mycologia **22**: 147. 1930.
Sorosporium hansfordii Ainsw. Proc. Linn. Soc. London **153**: 93. 1941.

Sori in the ovaries, partially concealed by the glumes, cylindrical, tapering at both ends, 8–15 mm. long, 1–1.5 mm. diam., each covered at first by a pale brownish false membrane which dehisces apically revealing a granular, black spore-mass intermixed with a number of long filaments of host tissue; on certain hosts the infected spikelets becoming more or less congregated. Spore-balls persistent, subglobose, oval to oblong, opaque, 52–150 x 37–110 μ, occasionally larger. Spores globose to broadly ellipsoid, or ovoid, mostly somewhat angular, 7.5–12 x 6.8–10.5 μ, with epispore around 1.5 μ thick; outer spores medium to deep reddish brown, verrucose on the free surface; inner spores subhyaline to pale yellowish, smooth.

On *Hyparrhenia dissoluta* (Nees) Hubb., Barberton Exp. Sta., Transvaal, South Africa, Apr. 23, 1914, A. O. D. Mogg, sub *Sorosporium everhartii* Ell. & Ev. (PRM 7770).

On *Hyparrhenia hirta* (L) Stapf, east bank of Tugela River, Natal, South Africa, May 1920, E. M. Doidge, type of *S. austro-africanum* (PRM 14168).

On *Hyparrhenia pilgeriana* Hubb., Kabaroni, Elgon, Uganda, Dec. 1933, C. G. Hansford, type of *S. hansfordii* (CMI 38989).

On *Hyparrhenia rufa* (Nees) Stapf, Leopoldville, Belgian Congo, May 18, 1906, H. Vanderyst 121, type (BR 266); Mbela, Belgian Congo, Mar. 10, 1906. H. Vanderyst 150, type of *S. wildemanianum* (BR 280); Kisantu, Belgian Congo, May 11, 1907, H. Vanderyst (BR 279); Dila, Belgian Congo, May 13, 1908, H. Vanderyst (BR 278); Kimpako, Belgian Congo, without date, H. Vanderyst (BR 281); without locality, Belgian Congo, 1910, H. Vanderyst (BR 276).

The redescription of *Sorosporium wildemanianum* given by Zundel (4) was based upon a collection on *Andropogon gabonensis* Stapf, which differs considerably from the type of this species, and the illustration accompanying the redescription represents neither the collection he cited nor any other collections found in the Botanical Garden of Brussels under that name.

The exsiccata specimen issued as *Sorosporium wildemanianum* in Sydow's Ustilagineen 414 is not this species, but an undescribed species of *Sphacelotheca* on *Cymbopogon*.

Sorosporium mutabile (Syd.) comb. nov.

Sphacelotheca mutabilis Syd. Ann. Myc. **35**: 24. 1937.
Sorosporium terrareginalense Zundel Mycologia **36**: 409. 1944.

Sori in the inflorescences, filiform, 5–10 mm. in length, concealed by leaf sheaths, later partially protruding, each covered at first by a thin, whitish false membrane which dehisces apically revealing a dark, powdery spore-mass intermixed with several fine filaments of host remnants. Spore-balls with spores firmly united in young sori, but becoming evanescent at maturity, opaque, globose to ellipsoid, or angular, 41–82 x 34–68 μ. Spores mostly polyhedral, occasionally subglobose, oval, or ovoid, 13–18 x 10.5–15 μ, deep to dark reddish brown, with epispore around 1.5 μ thick; outer spores finely but distinctly echinulate; inner spores punctate to finely echinulate.

On *Cymbopogon* refractus (R. Br.) A. Camus, Pennant Hills, New South Wales, Australia, June 1931, L. Fraser 118, type (CMI 37633).

Sorosporium hotsonii Zundel Mycologia **22**: 152. 1930.

Sorosporium harrismithense Zundel Mycologia **22**: 154. 1930.
Sorosporium flanaganianum Zundel Mycologia **22**: 155. 1930.
Sorosporium afrum Syd. Ann. Myc. **33**: 232. 1935.

Sori destroying the entire panicles, elongate-obovate, tapering at the apices, 1.5–3 cm. long, 5–8 mm. wide, partially concealed by leaf sheaths, each covered by a brownish false membrane which dehisces apically at maturity, but with lower part usually remaining surrounding the base of the sorus; spore-mass dark granular, intermixed with numerous threads of host tissue. Spore-balls opaque, globose to broadly ellipsoid, semi-persistent, 60–107 x 45–78 μ. Spores globose to oval, ovoid, or slightly angular, yellowish brown, uniformly colored, 9–12.5 x 8.5–11 μ; epispore 1–1.5 μ thick, densely but finely echinulate, echinulations less evident on inner spores.

On *Panicum laevifolium* Hack., Harrismith, Orange Free State, South Africa, Feb. 22, 1911, C. P. van der Merwe, type of *S. harrismithense* (PRM 1473); Randfontein, Transvaal, South Africa, Mar. 7, 1913, F. G. Allpars (PRM 6579).

On *Panicum* sp., Hopefield, Transvaal, South Africa, Feb. 2, 1910, without collector, type (PRM 704); Emmasdale, Heidelberg, South Africa, Jan. 15, 1910, without collector, type of *S. flanaganianum* (PRM 713).

Sorosporium versatilis (Syd.) Zundel on *Panicum longijubatum* Stapf is very similar to this species and can be distinguished from it only by having more slender sori (3–4 mm. diam.) and by having spores which are slightly larger (9–14 μ diam.), more variable in size, frequently more angular in shape, and more evidently verruculate. It is debatable whether such slight variation should be sufficient for the differentiation of species.

Zundel cited two collections in his original description of *Sorosporium flanaganianum* (3), but later (5) selected one of them as the type which is identical with *Sorosporium hotsonii*. The other collection is *S. versatilis* on *Panicum* sp.

Among the collections cited above, both spores and spore-balls vary considerably in size. In the type collection on *Hyparrhenia tampa*, the spores measure 9.5–15.5 x 9–14 μ and spore-balls 67.5–150 x 52.5–100 μ. The collection on *Hyparrhenia aucta* matches it fairly well. Other two collections on *Hyparrhenia dissoluta* and *Hyparrhenia* sp. have spores smaller than those of the type, with spores measuring mostly 9–12 μ in diameter and occasional ones attaining 14 μ. The spores of the collection on *Hyparrhenia cymbaria* are smallest, measuring mostly 8–11.5 μ in diameter. The average diameter of spores varies from around 10 μ to 12.5 μ. Such variation, however, does not appear to justify the separation of those collections into several species.

Externally, all these collections appear alike. The infection takes place at an early stage of the development of the inflorescences before the formation of peduncles and floral organs. All the infected individual inflorescences on a branch of the compound inflorescence thus become aggregated into a cluster. Sometimes, the development of the whole branch is prohibited and the growth is reduced to a cluster of smut sori surrounded by reduced leaves and leaf sheaths above the node.

SOROSPORIUM TEXANUM Zundel Mycologia **36**: 409. 1944.

On *Pennisetum nervosum* (Nees) Trin., Fort Brown, Brownsville, Texas, United States, Dec. 23, 1942, Hansel 52794, type (BPI).

The description of this species should be emended to include the occurrence of the infection in individual florets, forming sori 1.5–2.5 cm. long, in addition to the destruction of the entire inflorescences by the fungus.

SOROSPORIUM TEMBUTI Pole-Evans & P. Henn. Engl. Bot. Jahrb. **41**: 270. 1908. (Fig. 1,B).

Sorosporium healdii Zundel Mycologia **22**: 147. 1930.
Sorosporium proliferatum Zundel Mycologia **22**: 150. 1930.
Sorosporium clintonii Zundel Mycologia **22**: 153. 1930.

Sori in the inflorescences, each involving an ultimate inflorescence, inhibiting its development at a very early stage, thus causing all the infected inflorescences on one branch aggregated into a cluster, partially concealed by the spathe, cylindrical, 2–4 cm. long, 2–5 mm. diam.,

covered at first by a rather thick, persistent, yellowish false membrane which dehisces apically at maturity exposing a dark, granular spore-mass intermixed with a number of slender filaments of host origin. Spore-balls persistent, subglobose to oblong, opaque, 37.5–150 x 34–100 μ. Spores globose to oval, frequently somewhat angular or elongate; inner spores smooth, subhyaline to light brownish, 7.5–15.5 x 7–12 μ, wall 1.5–3 μ thick; outer spores deep reddish brown, occasionally subopaque, 9–16 x 8–14.5 μ, free surface verrucose and darker, wall 1.5–2 μ thick.

On *Hyparrhenia aucta* (Stapf) Stent, Waterval Boven, Transvaal, South Africa, Nov. 29, 1918, I. B. Pole Evans, type of *S. proliferatum* (PRM 11336).

On *Hyparrhenia cymbaria* (L.) Stapf, Kawanda, Uganda, Nov. 1943, C. G. Hansford (BPI).

On *Hyparrhenia dissoluta* (Steud.) Hubb., Waterkloof, Pretoria, Transvaal, South Africa, Apr. 14, 1916, I. B. Pole Evans, type of *S. clintonii* (PRM 9693).

On *Hyparrhenia* sp., Pretoria, Transvaal, South Africa, Mar. 7, 1916, I. B. Pole Evans, type of *S. healdii* (PRM 9732).

On *Hyparrhenia tampa* Anderss., Waterval Onder, June 1903, Burtt Davy, type (PRM 169).

THECAPHORA HAUMANI Speg. Rev. Argent. Bot. **1**: 150. 1925.

On *Iresine celosia* L., Turrialba, Costa Rica, Mar. 27, 1948, C. E. Chardon (BPI).

THECAPHORA PUSTULATA Clint. apud Chardon Rev. Agr. Puerto Rico **6**: 23. 1921.

On *Bidens pilosa* L., Turrialba, Costa Rica, Mar. 27, 1948, C. E. Chardon (BPI).

Testicularia minor (Juel) comb. nov.

Testicularia cyperi Klotz. var. *minor* Juel Bih. Till K. Sv. Vet.-Akad. Handl. **23**(10): 9. 1897.

Sori in the ovaries, narrowly ellipsoid to oblong, tapering at the apices, 3–7 mm. long, 1.5–3 mm. wide, each covered by a pallid, tough membrane of fungus tissue which is persistently attached to the sorus after its rupture from the apex; spore-mass black, compact, agglutinate. Spore-balls opaque, subglobose to ellipsoid, 45–115 μ long, each consisting of a peripheral layer of fertile spores and a central mass of thick-walled, subhyaline to yellowish, sterile parenchymatous cells averaging smaller than the spores. Spores globose to oval, present in different stages of development as indicated by the variation in color and size, from light olivaceous yellow to deep reddish brown, 13.5–22.5 x 12–19.5 μ; epispore 1.5–3 μ thick, smooth; endospore with granular content.

On *Rhynchospora gigantea* Link, Puerto Rico, P. Sintenis 6672 (NY).

This species is distinguished from *Testicularia cyperi* by the smaller sori and spore-balls, as well as by the larger and lighter colored spores. Its sori appear very similar to those of *Cintractia spicularum* (Juel) Racib.

This collection is also the type of *Cintractia krugiana* Magn.

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A New Needle-Cast Fungus on Chihuahua Pine[1]

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INTRODUCTION

During the autumn of 1949, the writer's attention was directed to a needle disease of Chihuahua pine, *Pinus leiophylla* Schlecht. et Cham., occurring in the State of Mexico, Republic of Mexico. Preliminary examination of these collections revealed that the pathogen was a member of the genus Hypoderma, of the family Hypodermataceae, commonly regarded as needle-cast fungi. Efforts to determine its specific identity, by use of a monograph of this family prepared by Darker (1932), disclosed that there are seven established species of Hypoderma on Pinus, but that the fungus on Chihuahua pine did not appear to be identical with any of them. Aid in identification was, therefore, sought by submitting specimens to Dr. G. D. Darker and to Dr. J. S. Boyce, with the result that each concurred in the opinion that the pathogen under consideration had not been described previously. Consequently, it seems desirable, at this time, to make known its characteristics as a contribution to knowledge of the mycotic flora of Mexico, about which, as yet, little is known.

STRUCTURE OF THE FUNGUS

Collections of affected needles made during October and November were found to bear fully-mature hysterothecia or fruiting bodies having well-developed ascospores. This was contrary to expectation, because the fruiting structures of most species of Hypodermataceae are known to mature in spring. It may be presumed that the period of greatest activity of most fungi would take place during the rainy season in areas in which there occurs an alternation of a rainy season with a dry one, and that such weather conditions would cause the fungi to become dormant following the advent of the dry season. Partial support for this interpretation, in the case of the pathogen under consideration, arises from the fact that when low relative humidities prevail the hysterothecia are inactive, but ascospores are discharged when moisture is available. Hysterothecia in a dry state, when viewed from above with low magnification, are ellipsoid-elongate or boat-shaped structures, and the presence of the orifice, or slit band, is difficultly discernible. If moistened, however, the hysterothecia open with an irregular fissure, and the opening may widen to the extent that the fruiting bodies appear discoid, quite as in the Phacidiales. Moreover, closure is effected promptly on drying.

[1]I am grateful to Jess P. Perry, Jr., Mexico City, Mexico, for his courtesies in collecting for me and supplying ample specimens of diseased needles. Special thanks, in addition, are extended herewith to Dr. G. D. Darker, Ben Venue Laboratories, Bedford, Ohio, and Dr. J. S. Boyce, School of Forestry, Yale University, New Haven, Connecticut, for their opinions relative to the identity of the pathogen.

The hysterothecia occur singly or in groups of two or three on isolated, small, greenish-yellow lesions on either leaf surface, Figs. 1 and 2. Even to the unaided eye, they appear as shiny, black, boat-shaped structures, which project prominently. In section, they are 1000–1500 μ long, 400–500 μ wide and 200–225 μ deep. The subcuticular plectenchymatous basal layer is 18–25 μ thick. The supporting mycelium is intracellular, densely fills the host cells beneath, and extends entirely through the leaf tissue. The covering layer (the labiae), together with the connate cuticle, is 36–50 μ thick. The hymenium is 175–200 μ thick. The asci are broadly saccate, rounded above, 8-spored, 130–175 × 35–40 μ, Fig. 4. The ascospores are hyaline, cylindrical, and the lower end is tapering, while the upper end is blunt. They are surrounded with a gelatinous envelope, approximately 5 μ thick, and measure 35–45 × 6–7 μ, Fig. 5. The paraphyses are filiform, inflated at the apex, and possess a gelatinous sheath.

The spermogonia have the same gross appearance as the hysterothecia, except that they tend to be smaller. The spermatia are bacillar, sheathed, and 4–5 × 0.8–1.0 μ, Fig. 7.

If hysterothecia are maintained on moist filter paper in a petri dish, the ascospores are liberated as a group by circumscissile rupture in the median region of the ascus. The ascospore group may then be partly contained within the thimble-like ascus tip, Fig. 3. In some cases, the asci remain intact, and the germ tubes extend to the exterior by penetrating the ascus wall. During germination, a septum forms, making the ascospores two-celled, Fig. 6, and a short-clubbed germ tube is produced.

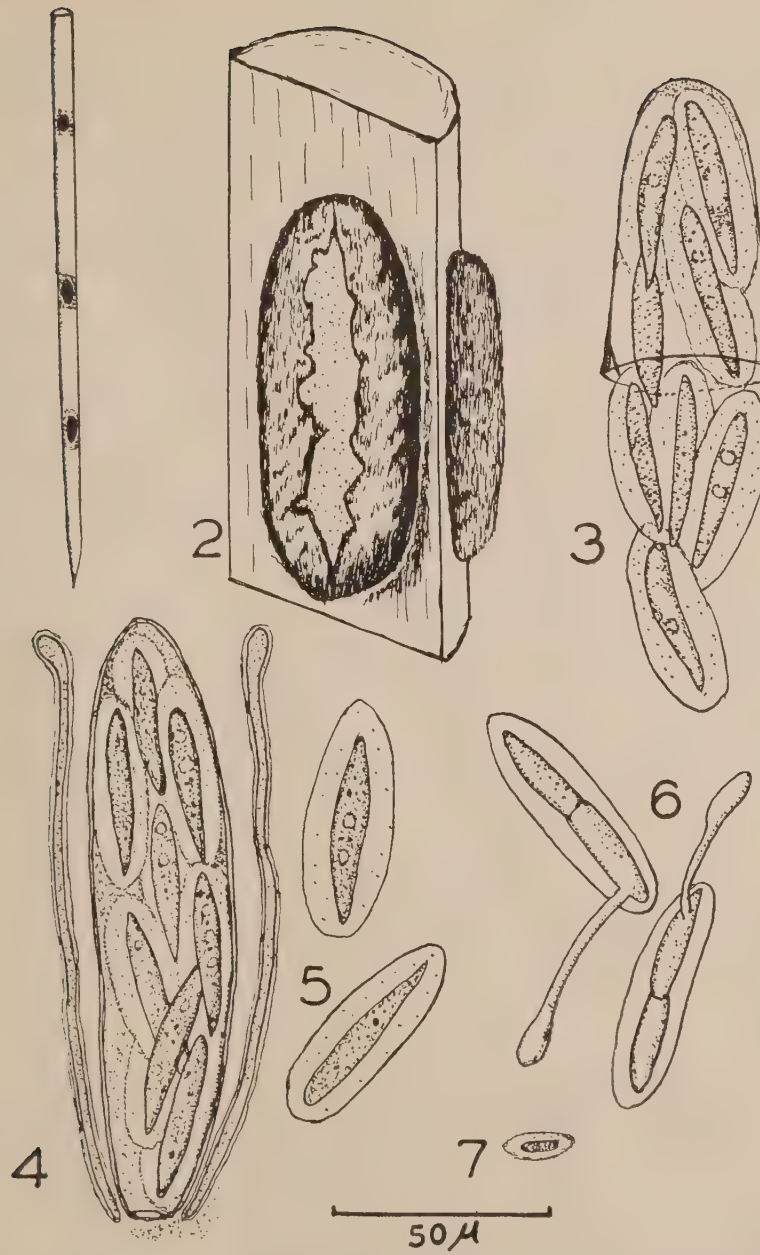
IDENTITY OF THE PATHOGEN

When the fungus on Chihuahua pine is compared with other species of Hypoderma on Pinus, it is found to be most like *H. saccatum* Darker. In his "Key to the Species of Hypoderma," Darker (1932) shows that *H. saccatum* has certain features, as follows, similar to those of the pathogen considered herein: (1) primordium of slit band not obvious, (2) paraphyses present, (3) hysterothecia conspicuous, shiny black, (4) spermagonia (pycnidia) conspicuous, and (5) asci with eight functional ascospores.

It differs from *H. saccatum*, however, as follows: (1) *H. saccatum* is known only on *Pinus edulis* Engelm., and (2) dimensions of the fruiting bodies and asci of *H. saccatum* are about two-thirds those of the fungus on Chihuahua pine. On the basis of these differences, the pathogen on Chihuahua pine is herewith described as a new species.

Hypoderma mexicanum sp. nov.

Hysterotheciis innatis dein erumpentibus, ellipsoideo-elongatis, conspicuis, atronitidis, amphigenis, in areis viridi-lutescentibus, navicularibus, 1000–1500 μ longis; longitudinale fissura irregulariter aperientibus, labiis exilibus atris; in transversalis sectionis aspectu subcuticularibus 400–500 μ latis; circiter 200–225 μ profundis; parenchymatico basilari strato 18–25 μ crasso; tegente strato atri pseudoparenchymatis epidermidisque 36–50 μ crasso. Ascis late saccatis, ad apicem obtuso-



FIGS. 1–7. *Hypoderma mexicanum*, sp. nov.—1. Sketch to indicate lesions bearing hysterothecia on needle of Chihuahua pine. 2. Enlarged diagramatic sketch, showing two hysterothecia of *Hypoderma mexicanum* sp. nov.; one hysterothecium is seen from above to indicate the opening at the slit band; and the other is seen laterally. 3. Group of ascospores together with the thimble-like ascue tip. 4. An ascus and paraphyses. 5. Fully-mature ascospores that had been liberated in the presence of moisture. 6. Germinating ascospores. 7. Spermatium (conidium). (Figures 3–7 drawn to indicated scale).

rotundatis, octosporis 130–175 × 35–40 μ. Paraphysibus simplicibus, filiformibus, in apice dilatis vel afflatis, muco involutis. Ascosporis cylindraceis vel clavatis, hyalinis, muco 4–5 μ crasso imvolutis, 35–45 × 6–7 μ. Spermogoniis atronitidis, conspicuis, subcuticularibus, magnis. Spermatiis hyalinis 4–5 × 0.8–1.0 μ. Hab. in foliis Pini leiophyllae Schlecht. et Cham., Mexico, mense Octobre ac Novembre. Jess P. Perry legit.

Specimens have been deposited in the Farlow Herbarium, Harvard University, and in the herbarium of the Division of Mycology and Disease Survey, U. S. Department of Agriculture.

DISCUSSION

There is lack of agreement in the accounts which deal with studies of the pathogenicity of members of the Hypodermataceae. The pathogenicity of the widely-distributed *Lophodermium pinastri* (Schrad.) Lev. remains to be established unequivocally. Weir (1916) concluded that *Elytroderma deformans* (Weir) Darker is pathogenic on western yellow pine. Darker (1932) secured evidence that *Bifusella faulii* Darker, *Hypoderma desmazierii* Duby, *Hypodermella laracis* Tubeuf, and *H. concolor* (Dearn.) Darker are pathogenic.

In the eastern United States, *Hypoderma lethale* Dearn. occurs on green needles of pitch pine, slash pine, loblolly pine, short-leaf pine, and Virginia scrub pine. However, its pathogenicity has not been established experimentally. Evidence of pathogenicity of *H. mexicanum* rests solely upon the occurrence of its hysterothecia on well-defined lesions on green needles.

Studies designed to elucidate the life history and developmental morphology of *H. mexicanum* and Hypodermataceae generally, similar to a study by Jones (1935) dealing with *Laphodermium pinastri*, are much needed.

Only incidental mention has been made hitherto of the presence of gelatinous envelopes on ascospores of Hypodermataceae. Such envelopes may well be adaptations which function to cause the spores to adhere to the suscept and also to provide adequate moisture for penetration of the germ tube when infections are being initiated.

SUMMARY

This account deals with the structure and identity of a fungus collected near Mexico City, Mexico, and regarded as a pathogen on Chihuahua pine, *Pinus leiophylla*. Its structural features most closely resemble those of *Hypoderma saccatum* Darker, but it is here regarded as distinct and designated *Hypoderma mexicanum* sp. nov.

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Florida Hydnums

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These fungi bear their spores on teeth, warts or folds. The sporophores are found on leaf-mold in woods, on dead wood or on diseased wood in living trees. A few are fleshy and edible but most of them are tough and inedible. Several cause heart-rot.

H. J. Banker studied the hydnums of N. A. for many years and published several articles on the pileate species, notably one in Vol. 12 of the Torrey Club Memoirs, which contains ten pages of bibliography. His large collection was donated to the N. Y. Botanical Garden, where his work was chiefly done.

W. C. Coker followed Banker and devoted his attention to the pileate species of N. C., publishing two fine papers with excellent halftone illustrations in Jour. Mitchell Soc. **34:** 163 and **41:** 270. His work is of special value to Fla. students.

L. W. Miller confined his studies chiefly to the species occurring in Iowa, although treating the genera for all of North America. Shifting from the American Code used by Banker to the International Code necessitated several changes in nomenclature. Resupinate species were also studied for a limited area. His papers were published in Vols. 25–27 of Mycologia, one devoted to the North American genera and four to the Iowa species. I cannot accept the substitution of *Mycoacia* Donk for *Oxydontia* Miller, as published in "The Hydnaceae of Iowa" by Miller and Boyle, 1943.

Many resupinate species found in Florida are still unstudied. The present paper, however, may serve as an introduction to the subject and stimulate further study and field work.

Appended to this paper is an account of my collecting in and about Gainesville during January and February, 1949.

HYDNACEAE

Hymenium borne on downward-pointing spines, teeth or warts which have not arisen by breaking up of pores. Genera like *Irpex* and *Hydnochaete* thus go to the Polyporaceae and *Phlebia* to the Xylophagaceae with *Merulius*.

For Banker's key see Mem. Torr. Club **12:** 103,4. 1906; and for Miller's see Mycol. **25:** 289. 1933.

KEY TO FLORIDA GENERA

Context dark; spores rough; usually brown; hymenophore stipitate, terrestrial.
- Hymenophore fleshy ..... 1. Hydnum
- Hymenophore fibrous, tough ..... 2. Calodon

Context pale, spores usually smooth, hyaline or slightly colored.
- Teeth arising directly from the substratum ..... 3. Mucronella
- Teeth developed on a distinct hymenophore.
  - Fructification resupinate.
    - Cystidia or setae present ..... 4. Odontia
    - Cystidia or setae wanting.
      - Warts short, hemispherical, cylindrical, or subulate and fragile ..... 5. Grandinia
      - Teeth or spines conspicuous, slender, usually terete ..... 6. Oxydontia

Fructification reflexed to stipitate.
Terrestrial, mesopodous.....7. Dentinum
Epixylous, not mesopodous.
Abundantly branched or pulvinate.....8. Hericium
Reflexed or dimidiate to laterally stipitate.
Teeth minute, 0.25 mm. long.....9. Grandinioides
Teeth conspicuous, longer.....10. Steccherinum

1. HYDNUM L. *emend.* S. F. Gray

This includes *Sarcodon* Quél. For description see Mycol. **25:** 299. 1933.

KEY TO FLORIDA SPECIES

Pileus velvety.....*H. alachuanum*
Pileus strigose.....*H. cristatum*
Pileus squamulose.....*H. fennicum*

H. alachuanum Murr. Bull. Torr. **67:** 281. 1940.—Described from Gainesville, where it is frequent in oak or pine woods.

H. cristatum Bres. See Coker, Mitchell **34:** 169. 1919.—Rare in woods about Gainesville and DeLeon Springs. Found on the ground in mixed woods from Conn. to Fla.

H. fennicum (Karst.) Sacc. See Coker, Mitchell **41:** 272. 1926.—Described from Finland and found on the ground in mixed woods from Mass. and Ky. to Fla. Rare about Gainesville under laurel oak and found in oak-pine woods in Marion Co.

2. CALODON Quél.

This genus includes both *Phellodon* Karst. and *Hydnellum* Karst., according to Miller. For his description see Mycol. **25:** 300. 1933.

KEY TO FLORIDA SPECIES

Pileus zonate.....*C. zonatum*
Pileus azonate, velvety.
Stipe rusty in color.....*C. ferrugipes*
Stipe spongy, not rusty.....*C. velutinum*
Stipe neither rusty or spongy.
Stipe blackening.....*C. diabolus*
Stipe not blackening.....*C. amicum*

C. amicum Quél. See Coker, Mitchell **34:** 192. 1919.—Rare in hammocks about Gainesville. Also collected in the ravine in Gold Head Branch Park, Clay Co. Described from Eur. as *Hydnum amicus* Quél. *H. vellereum* Pk. is not distinct and *H. putidum* Atk. is very close.

C. diabolus (Bank.). See Coker, Mitchell **34:** 182, 1919, and Banker, Mycol. **5:** 194. 1913.—Frequent about Gainesville in oak woods and collected in Columbia and Marion Counties in oak or mixed woods.

C. ferrugipes (Coker). See Jour. Mitchell Soc. **34:** 188. 1919.—Common in oak or mixed woods about Gainesville and also collected in Columbia Co. Described from N. C.

C. floriforme (Schaeff.). See Bres. Icon. Myc. **22:** *pl.* 1052. 1932.—Described from Bavaria and found on the ground in dry woods in Eur. and eastern N. A., from New Eng. to Fla. and Ala. Frequent about Gainesville under laurel oaks. See Banker's memoir. *C. aurantiacum* (A. & S.) Karst. is a synonym.

C. velutinum (Fr.) Quél. See Coker, Mitchell **34:** 183. 1919.—Described from Eur. and found on the ground in fairly dry woods from Conn. to Fla. and westward to O. and Ala. Rare about Gainesville in frondose woods. *H. spongiosipes* Pk. is not distinct.

C. zonatum (Fr.) Quél. See Coker, Mitchell **34:** 185, 1919.—Described from Eur. and found on the ground in dry woods from N. Y. and Ia. to Fla. and Ala. Abundant about Gainesville under oaks and other frondose trees in hammocks or groves.

3. Mucronella Fr.

For description of genus see Mycol. **25:** 295. 1933.

M. aggregata Fr. See Miller, Mycol. **26:** 215. 1934.—Described from Eur. and found in temp. N. A. southward to Fla. Rare about Gainesville on hardwood logs in hammocks.

M. plumosa (Duby). See Sacc. Syll. Fung. **6:** 475. 1888.—Described from Eur. and found on dead wood from New Eng. to Fla. Common about Gainesville on dead wood of oak, linden, sweet gum, etc. It differs from *M. aggregata* in having the tips of the teeth plumose.

4. Odontia Pers. *emend.* Fr.

Including *Kneiffia* Fr. For description see Mycol. **25:** 292. 1933; and for key to species see Mycol. **26:** 13. 1934.

O. Archeri (Berk.) Wakefield.—Collected a few times during Jan. and Feb., 1944, on decorticated logs of loblolly pine in low woods near Gainesville. Det. by Linder. Reported by me in Mycologia, 1944.

O. arguta (Fr.) Quél. See Miller, Mycol. **26:** 26. 1934.—Described from Eur. and found on dead wood of conifers and hardwoods in temp. N. A., westward to Ia., where it is abundant, and southward to Fla., where it seems to be rare. *O. alutacea* Bres. is not distinct and *Hydnum caryophylleum* B. & C. is close, according to Miller. On hornbean at Gainesville.

O. bicolor (Alb. & Schw. *ex* Fr.) Bres. See Miller, Mycol. **26:** 27. 1934.—Described from Eur. and found on dead wood from Can. to Fla. and westward to Ia. and La. The specimens Miller saw from Fla. were labeled *Grandinia granulosa* Fr.

O. setigera (Fr.) Miller, Mycol. **26:** 19. 1934.—Described from Eur. and widely distributed in temp. N. A. on both frondose and coniferous wood. Common about Gainesville on dead wood of oak, sweet gum, pine, etc. Fries described it under *Kneiffia*.

5. Grandinia Fr.

For description of genus see Mycol. **25:** 291. 1933.

C. chrysocreas (B. & C.) Lloyd. See Sacc. Syll. Fung. **6:** 618. 1888, under *Corticium*.—Described from pine trunks in S. C. and Ala. Rare about Gainesville on pine logs. It is yellow when fresh with a white to fulvous papillate hymenium. See *Corticium* in the Thelephoraceae, where it was formerly placed.

G. fasciculare (B. & C.). See Sacc. Syll. Fung. **6:** 473. 1888.—Described from S. C. and found on tupelo, etc., in temp. N. A., south-

ward to Fla. Common about Gainesville on dead wood of oak, hornbeam, etc.

6. OXYDONTIA Miller

For description of genus see Mycol. **25:** 294. 1933.

O. fragilissima (B. & C.) Miller, Mycol. **25:** 364. 1933.—Described from S. C. and found in temp. N. A., southward to Fla. Common about Gainesville on rotten frondose logs in woods and also collected at Bartow on dead lemon branches. Very fragile when dry and soon fading. The hymenium is ceraceous. *H. floridanum* Berk. & Cke. is said to be near this species. It is orange-red when fresh with a white margin. Described from Gainesville on dead branches.

7. DENTINUM S. F. Gray

For description of genus see Mycol. **25:** 298. 1933.

D. repandum (Fr.) S. F. Gray. See Coker, Mitchell **34:** 166. 1919.—Described from Eur. and found in mixed woods in temp. N. A., southward to Fla. and Calif. Common in hammocks about Gainesville and also collected in Union Co. A white form is occasionally found.

8. HERICIUM Pers. *ex* S. F. Gray

For description of genus see Mycol. **25:** 298. 1933.

H. caput-ursi (Fr.) Bank. See Bank. Mem. Torr. Club **12:** 118. 1906.—Described from Eur. and found on beech and certain other frondose trees from Can. to Fla. in the eastern U. S. Rare about Gainesville on diseased oak trunks in hammocks. It differs from *H. erinaceus* in having short branches from which short teeth are pendent. It may not be distinct from the true *H. coralloides* Scop. *ex* S. F. Gray. What we usually call *H. coralloides* is more correctly *H. laciniatum* Leers. Atkinson has excellent halftones of all three species in his Stud. Am. Fungi.

H. erinaceus (Fr.) Pers. See Coker, Mitchell **34:** 176. 1919.—Described from Eur. and found on diseased trunks of frondose trees from N. Y. and Wisc. to Fla. and Mex. Frequent about Gainesville on water oak, sweet gum, etc. Also collected at Floral City on turkey oak. Banker called it *Manina cordiformis* Scop.

9. GRANDINIOIDES Bank.

For description of genus see Mem. Torr. Club **12:** 179. 1906.

G. flavum (Sw.) Bank. Mem. Torr. Club **12:** 179. 1906.—Described from W. I. and found on dead wood in trop. Am., Fla. and La. Frequent in hammocks about Gainesville on dead oak twigs above ground and also collected near Santa Fé, Alachua Co. Swartz placed it in *Peziza;* Berkeley recognized it as a *Hydnum.*

10. STECCHERINUM S. F. Gray

For description of genus see Mycol. **25:** 296. 1933.

KEY TO FLORIDA SPECIES

Pileus large, strigose, white to reddish ..... *S. pulcherrimum*
Pileus small to medium.
  Stipe present ..... *S. adustum*
  Stipe wanting.
    Pileus white, glabrous ..... *S. subrawakense*
    Pileus ochraceous, subtomentose ..... *S. ochraceum*
    Pileus not as above.
      Spores 2 μ long ..... *S. Westii*
      Spores 4 μ long ..... *S. rawakensi*

S. adustum (Schw.) Bank. See Coker, Mitchell **34:** 180. 1919.—On dead branches from New. Eng. to Fla. and westward to Ia. and Ala. Common about Gainesville on dead frondose wood in hammocks.

S. ochraceum (Pers. *ex* Fr.) S. F. Gray. See Coker, Mitchell **34:** 179. 1919, under *S. rhois* (Schw.) Bank. Described from Eur. and found on dead wood from Can. to Fla. and westward to Ia. and Tex. Common about Gainesville on oak, sweet gum, hornbeam, pine, etc. Also found at Citra. Banker says *S. laeticolor* is easily distinguished by its soft spongy substance and reddish color when young and fresh. *H. ciliolatum* B. & C., found on *Magnolia glauca* in S. C., is said to be near resupinate *S. ochraceum* but with very different teeth.

S. pulcherrimum (B. & C.) Banker. See Coker, Mitchell **34:** 178, and **41:** 285.—On dead logs from New Eng. to Fla. and westward to O. and La. Common about Gainesville on oak logs. Collected on pine logs at Green Cove Springs, Windermere, and on Merritt Island.

S. rawakense (Pers.) Bank. See Miller, Mycol. **27:** 363. 1935.—Rare about Gainesville on dead wood of oak and linden in hammocks. First found in Rawak, Borneo, and later collected in the W. I., S. A., and Africa. *H. reniforme* (B. & C.) described from Cuba and reported from Honduras and La., is not distinct.

S. subrawakense Murr. Bull. Torr. **67:** 281. 1940.—Described from near Gainesville, Fla., on a hardwood log in a hammock.

S. Westii Murr. Bull. Torr. **67:** 281. 1940.—Described from Gainesville on an oak log in woods. Also found at Hawthorne on a hardwood log.

COLLECTING IN JANUARY AND FEBRUARY, 1949

The temperature at Gainesville in November, 1948, was the highest on record, and that of December several degrees above normal. Although conditions for the growth of fungi seemed almost ideal during the greater part of December, the well-established species remained dormant. However, quite a number of species that fruit in cool weather were collected, a notable exception being *Armillaria mellea*.

On Jan. 1, 1949, Dr. G. F. Weber made a collection in low woods at Hawthorne, a few miles east of Gainesville, which included *Grifola cristatiformis*, *Fomitiporia dryophila*, *Pogonomyces hydnoides*, *Daedalea ambigua*, *Clavaria flava* and *C. unicolor*, *Boletus brevipes*, *Lactarius Gerardii*, *Laccaria laccata*, *Tricholoma russula*, *Amanita cothurnata*, three species of *Russula*, two species of *Hygrophorus*, several species of *Cortinarius*, and *Panaeolus solidipes*.

On Jan. 16, I found a few fungi in a dry live-oak thicket south of Payne's Prairie, near Gainesville, including *Laccaria amethystea*, a

pink *Russula*, two species of *Cortinarius* and *Ithyphallus Ravenelii*. It was so dry I did not expect to see any fleshy species.

COLLECTING IN GAINESVILLE

Jan. 1–2.—The year opened cool and frosty, becoming mild on the second day, when I collected *Cordyceps agariciformis*, *Amanita roanokensis*, *Armillaria caligata floridana*, two common species of *Cortinarius* and a large branched *Clavaria*.

Jan. 3–6.—Warm or mild, clear or cloudy, no rain until the night of Jan. 6. Mostly too dry for fungi. The few picked up included *Hexagona brasiliensis*, *Laccaria laccata*, *Boletus brevipes*, *Hypholoma fasciculare*, three species of *Russula*, and a bitter species of *Flammula* on pine lumber.

Jan. 7–27.—Chilly to warmer, becoming perfectly delightful and fair for three weeks. Too dry for fungi. The only ones seen were *Hypholoma fasciculare*, *Cortinarius equestriformis*, *Cordyceps agariciformis*, and three common species of *Cortinarius*.

Jan. 28–30.—Showers fell on these three days but they were too light to have much effect after three weeks of drought. No fungi were collected except *Pleurotus ostreatus*, on a magnolia log in the woods.

Jan. 31.—There was a gentle, warm rain and two fleshy fungi were seen; *Boletus subvelutipes* on a lawn and a species of *Coprinus* in cultivated soil near a new hedge of Japanese box.

January was unusually dry and warm with much sunshine and no storms. It afforded a rest period for fleshy fungi such as one finds in Cuba during the winter.

Feb. 1–8.—The first day was cool and sunny but on the second it rained all day, totaling 2.6 in. The other days were warm and cloudy with showers. I found *Hypholoma fasciculare*, *Lentinus velutinus*, *Auricularia auricularis*, *Agaricus cylindriceps*, and a species of *Mycena* at the base of a young pine. It may be *M. viscosa* Maire or something new. On Feb. 6 the following were seen: *Pleurotus ostreatus*, *Hydnum floriforme*, *Agaricus projectellus*, *Tricholoma terreum* and *T. imbricatum*, a common fulvous species of *Cortinarius* and two common red species of *Russula*. So far, only cool-weather species had appeared. On Feb. 8 I added others to the list: *Stropharia bilamellata*, *Russula pectinata*, *Polyporus arcularius*, *Boletus brevipes*, *Leotia lubrica*, *Clathrus columnatus*, *Pluteus cervinus* and *Marasmius spongiosus*.

Feb. 9–10.—Warm, clear and sunny at first but developing into an "April day" with spells of wind, sunshine and rain, then westerly winds and cooler. I found fresh fruit-bodies of *Pycnoporus sanguineus*, *Boletus brevipes*, *Galera crispa*, *Clavaria flava*, *Tricholoma terreum*, *Claudopus nidulans*, *Psathyrella disseminata*, *Stropharia coronilliformis*, *Inocybe subprominens*, *Stereum subpileatum*, *Scleroderma cepa*, *Cortinarius lilacinus*, *Psathyra subvestita* and a large woodland species of *Agaricus*.

Feb. 11–12.—Cool and clear with northerly winds. Too cold for fungi, especially at night. Wide search was made for *Lepiota Morgani* and other summer species but they were still dormant in spite of favorable weather. No *Armillaria mellea* had appeared during the winter because, when it became cool enough the weather was too dry, and

when it became wet enough it was too warm. *Cryptoporus volvatus* was found for the first time in Florida, on a dead standing loblolly pine in mixed woods at Gainesville. It is unique among the polypores.

Feb. 13–16.—The wind became southerly, bringing warm weather and a few clouds but no rain. While the past few days were too cool for fungi, the lack of rain still prevented development. Even *Boletus brevipes* had disappeared, along with *Pleurotus ostreatus*.

Feb. 17–20.—The wind shifted to northeast, bringing cooler weather with clouds and a threat of rain. On the afternoon of Feb. 18 it became warmer and there was a light shower. Then, with the wind southwest, it was warm and partly cloudy but still too dry for fungi, although perfect for grass and azaleas. On the lawns I found nothing; in mixed woods only *Pluteus cervinus* and a large species of *Agaricus;* and in an azalea bed *Agaricus pocillator*.

Feb. 21–28.—Wind shifted back to northeast, mild, clear to cloudy, too dry for fungi. On Feb. 23 it became cooler because of a northwest wind, which continued for several days. A good rain fell on the afternoon of Feb. 27, followed by clear, cool weather. The only fungi found were *Hypholoma fasciculare*, *Xerotus lateritius* and *Lentinus strigosus*. None appeared on the lawns.

CONCLUSION

Although we enjoyed the balmiest winter for over sixty years the species of fleshy fungi fruiting normally during the summer remained dormant. The habits of millions of years are not easily broken. A considerable number of our cool-weather species appeared but their abundance was adversely affected by periods of dry weather.

Physiological Studies of Some Phytophthoras

III. Carbon Requirements*

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INTRODUCTION

Knowledge of which organic compounds, in addition to mineral salts, are necessary for the nutrition of fungi, is of great practical importance to all mycologists. It is well known that fungi vary in response to different carbon compounds employed to fortify synthetic media.

In general, fungi, like bacteria, prefer carbohydrates as food sources. A survey of the literature shows that no particular sugar provides the best source of carbon and energy for all micro-organisms, although it is probable that most micro-organisms, excluding algae, can use most sugars to some extent. Glucose appears to be the most favorite carbohydrate of fungi. It may be utilized first from a solution containing a mixture of sugars, or it may even be the only one removed. *Fusarium lini*, however, is said to be unable to utilize glucose (Tochinai, 1926). Variation among species in their ability to utilize sources of carbon is further shown by the observations of a number of other workers. Schade (1940) found that *Apodachlya brachynema* grew well on dextrose, laevulose, and sucrose but was unable to utilize maltose and galactose, whereas *Leptomitus lacteus* used none of these sugars. Whiffen (1945) noted that *Saprolegnia ferax*, *Achlya flagellata*, *Thraustotheca clavata* and *Aphanomyces stellatus* were able to use glucose, maltose, starch and glycogen, while *Dictyuchus monosporus* utilized only glucose. Bhargava (1945) found mannose to be a good carbon source for *Saprolegnia monoica* and *Brevilegnia gracilis* while it was useless for *Achlya* sp., *Isoachlya anisospora* var. *indica*, and *Saprolegnia delica*.

In the order Pythiales, only the carbon requirements of the genus *Pythium* have been investigated (Saksena, 1940, and Saksena and Mehrotra, 1949). Little work of this kind seems to have been done on the genus *Phytophthora*.

The investigations reported herein were carried on to determine by quantitative measurements the relative growth supporting values of several different carbon compounds for the following species of the genus *Phytophthora:*

1. *Phytophthora cactorum* (Leb. et Cohn) Schroet.
2. *Phytophthora citricola* Saw
3. *Phytophthora fagi* Hart
4. *Phytophthora meadii* Mc Rae
5. *Phytophthora paeoniae* Cooper et Porter
6. *Phytophthora parasitica* Dastur
7. *Phytophthora parasitica* Dastur var. *nicotianae* Tucker

*Part of the thesis approved for the degree of Doctor of Philosophy in the University of Allahabad.

8. *Phytophthora parasitica* Dastur var. *piperina* Dastur
9. *Phytophthora pini* Leonian
10. *Phytophthora Richardiae* Buisman

Nos. 1, 2, 4 and 5 were obtained from Centraal Bureau voor Schimmelcultures, Baarn, Holland; Nos. 9 and 10 were obtained from Dr. John T. Middleton and the rest were obtained from The Indian Agricultural Research Institute, New Delhi.

METHODS

The methods and technique employed in this investigation were almost the same as described earlier (Mehrotra, 1950). The basal medium consisted of 0.5 gm. each of KH_2PO_4, $MgCl_2.6H_2O$ and K_2SO_4, and 2.0 gms. of NH_4NO_3, 2000 international units of thiamine, and 1000 c.c. of distilled water. Carbon from whatever source was introduced in quantities so as to give a concentration equivalent to 4000 mgs. carbon per liter. Dextrin, inulin and soluble starch were taken equal in weight of dextrose because of their unknown constitution. The hydrogen-ion concentration of the nutrient solutions was adjusted to pH 6.5 in each case.

A particular substance was confirmed to be suitable only when the fungus grew on it in subsequent transfers. This was done, in each case, by dissecting a portion of the mycelium inside the flask with the help of a sterile platinum needle and transferring aseptically to another set of flasks containing the same medium.

EXPERIMENTAL

Series 1.—The following carbon compounds were added singly to the basal medium before autoclaving. The basal medium alone acted as control.

CARBOHYDRATES

Sugars				Non-Sugars
Monosaccharides		Disaccharides	Trisaccharides	Polysaccharides
Pentoses	Hexoses	Sucrose Lactose Maltose	Raffinose	Soluble starch Inulin Dextrin
Arabinose Rhamnose Xylose	Dextrose Laevulose Galactose Mannose			

ALCOHOLS

Trihydric	Tetrahydric	Hexahydric
Glycerine	Erythrite	Dulicte Mannite Sorbite

GLUCOSIDE

Amygdalin

TABLE 1. *Dry weights (in mgs.) of the fungal colonies grown at 25° C. on 25 c.c. of the basal medium supplemented separately with the various carbohydrates. The period of incubation was 16 days. The relative hydrogen-ion concentrations of the nutrient media after the growth of the fungi are given in brackets below the dry weights.*

Fungi	Basal medium (Control)	Arabinose	Rhamnose	Xylose	Galactose	Dextrose	Laevulose	Mannose	Lactose	Maltose	Sucrose	Raffinose	Dextrin	Inulin	Soluble starch
Phytophthora cactorum	(6.5)	13.3 (3.2)	14 (3.2)	10 (3.8)	15 (3.4)	24 (3.1)	12 (4.1)	9 (4.0)	20 (4.6)	30 (3.0)	32 (2.8)	15 (3.2)	15 (3.2)	20 (3.6)	30 (3.0)
P. citricola	(6.5)	17.5 (3.8)	15 (3.4)	10 (3.8)	20 (3.0)	23 (2.9)	20 (2.4)	10 (3.2)	18.7 (4.6)	26 (3.0)	30 (2.8)	10 (3.8)	16.6 (3.0)	15 (4.5)	27 (3.1)
P. fagi	(6.5)	10 (4.0)	16.6 (3.7)	5 (4.4)	20 (3.4)	22 (3.2)	5 (4.8)	5 (5 4)	15 (4.2)	22 (3.2)	32 (3.0)	7 (4.0)	20 (3.2)	20 (4.2)	22 (3.2)
P. meadii	(6.5)	16.5 (3.2)	12 (3.4)	7.9 (3.6)	20 (3.2)	20 (3.2)	17 (3.8)	10 (3.1)	17.5 (4.5)	24 (3.1)	32 (3.0)	13.3 (3.2)	13.3 (3.0)	11.6 (3.9)	20 (3.1)
P. paeoniae	(6.5)	13.3 (3.7)	20 (3.9)	8 (3.4)	20 (3.4)	24 (3.2)	20 (4.2)	8 (3.5)	20 (4.4)	25 (3.1)	25 (3.4)	8.3 (3.8)	14 (3.1)	16 (4.0)	26 (3.1)
P. parasitica	(6.5)	15 (4.0)	17.5 (3.4)	10 (3.0)	20 (3.8)	22 (3.4)	13 (4.4)	10 (3.4)	15 (4.5)	25 (3.2)	25 (3.6)	8.3 (3.8)	12 (3.2)	15 (4.8)	24 (3.1)
P. parasitica var. *nicotianae*	(6.5)	20 (3.4)	20 (3.4)	9 (3.2)	20 (3.2)	20 (3.0)	18 (4.0)	10 (3.2)	13.3 (4.6)	22.5 (3.1)	28 (3.4)	5 (4.6)	10 (3.1)	18 (4.2)	27 (3.0)
P. parasitica var. *piperina*	(6.5)	15 (4.0)	12.5 (4.8)	10 (3.2)	19 (3.2)	22.5 (3.4)	5 (5.6)	15 (3.4)	14 (4.5)	24 (3.2)	25 (3.3)	14 (3.2)	11 (3.4)	22 (4.0)	20 (3.4)
P. pini	(6.5)	10 (4.6)	10 (4.0)	11.6 (3.0)	20 (3.0)	22 (3.0)	20 (3.4)	15 (3.0)	16 (4.0)	26 (2.8)	32 (3.1)	16.6 (3.6)	25 (3.0)	22 (3.4)	25 (3.1)
P. Richardiae	(6.5)	15 (3.4)	13 (3.4)	10.5 (3.8)	15 (4.2)	22 (3.4)	5 (5.8)	15 (3.8)	14.5 (4.6)	28 (4.0)	30 (3.1)	10 (3.9)	14 (3.4)	20 (3.6)	27.5 (3 6)

Various media thus obtained were inoculated with the species of *Phytophthora* under investigation. The results are summarized in tables 1 and 2 and, in addition, those concerning *P. cactorum* are graphically represented in fig. 1.

TABLE 2. *Dry weights (in mgs.) of the fungal colonies grown at 25° C. on 25 c.c. of the basal medium supplemented separately with the glucoside and the various alcohols. The period of incubation was 16 days. The relative hydrogen-ion concentrations of the nutrient media after the growth of the fungi are given in brackets below the dry weights.*

FUNGI	BASAL MEDIUM (Control)	ALCOHOLS					GLUCOSIDE
		Glycerine	Erythrite	Mannite	Dulcite	Sorbite	Amygdalin
Phytophthora cactorum	..... (6.5)	24.5 (3.2)	12.5 (3.8)	15 (3.6)	13.3 (3.8)	22 (3.2)	7 (4.0)
P. citricola	..... (6.5)	23.3 (3.1)	17.5 (5.1)	8.6 (3.4)	12 (4.0)	18 (3.4)	5 (4.4)
P. fagi	..... (6.5)	20 (4.6)	10 (4.6)	16.6 (3.2)	20 (3.8)	20 (3.6)	10 (3.8)
P. meadii	..... (6.5)	18.3 (4.6)	11.6 (3.8)	13.3 (3.2)	15 (3.4)	15 (3.4)	5 (4.5)
P. paeoniae	..... (6.5)	20.5 (3.4)	15 (4.6)	5.0 (4.8)	15 (4.0)	15 (3.8)	5 (4.0)
P. parasitica	..... (6.5)	22 (4.0)	10 (4.8)	10 (4.9)	9.5 (4.0)	16 (4.0)	7 (4.0)
P. parasitica var. *nicotianae*	..... (6.5)	20 (3.8)	12 (3.8)	9.5 (5.0)	10 (3.6)	14 (4.6)	5 (4.1)
P. parasitica var. *piperina*	..... (6.5)	20 (4.6)	10 (4.8)	10 (4.9)	17 (4.0)	15 (4.4)	5 (4.0)
P. pini	..... (6.5)	22 (3.1)	10 (4.0)	8.3 (4.0)	8.5 (4.8)	18 (3.4)	5 (4.4)
P. Richardiae	..... (6.5)	16.6 (4.8)	13 (3.8)	5.4 (4.9)	13.3 (3.4)	20 (3.4)	10 (3.7)

The data recorded in the tables show that there was no growth in the control. In general, the pentoses appeared to support poor growth of the fungi investigated. Xylose appeared to be much less effective than arabinose and rhamnose. Among the hexoses, dextrose proved to be the best source of carbon, and the remaining three sugars were used mostly in the following order of their utility: galactose, laevulose and mannose.

Of the three disaccharides tested, sucrose and maltose supported very good growth. Lactose proved to be a mediocre source.

The trisaccharide raffinose acted as a poor source of carbon.

Of the polysaccharides, soluble starch was the best source of carbon. Inulin and dextrin were poorer sources of carbon.

Alcohols, in general, were poorer sources of carbon than the carbohydrates. Glycerine supported the best growth. Sorbite came next to glycerine while erythrite, mannite and dulcite were almost equally effective as sources of carbon.

Amygdalin, a glucoside, acted as a poor source of carbon.

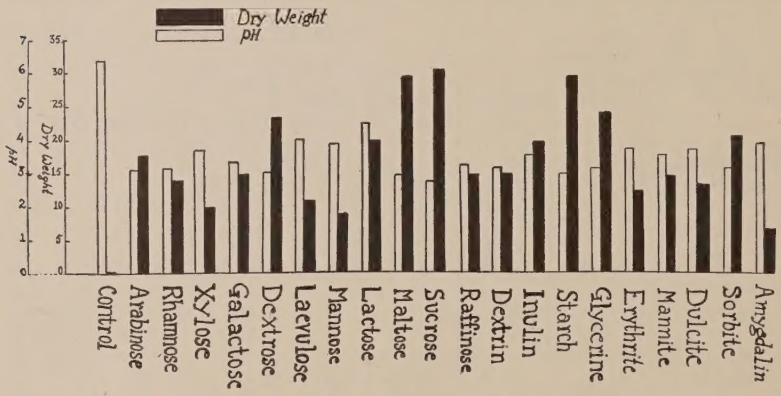

FIG. 1.—Dry weights (in mgs.) of the colonies of *Phytophthora cactorum*, grown for 16 days in the basal medium supplemented with the various carbon compounds singly, and change in pH value of the nutrient media after growth.

Series II.—In order to lessen the risk of various carbon compounds being hydrolysed in the presence of the basal medium during autoclaving, the solutions of various carbon compounds and the basal medium were autoclaved separately and mixed after cooling. The flasks were then incubated for 72 hours, and the sterile ones inoculated with fungi. The results were practically the same as obtained in series I.

DISCUSSION

Utilization of various carbon compounds depends on the ability of the fungi either to assimilate them directly or to convert the complex carbon compounds into forms that can be used directly. In the latter process the enzymes associated with the organism play an important rôle. Those carbon compounds which can be assimilated most readily or can be oxidized with the least expenditure of energy stored in the compound appear to constitute the food of first choice for fungi.

Pentoses (arabinose, rhamnose and xylose) have generally been regarded as poor sources of carbon, though Moore (1937) found that in the case of *Phymatotrichum omnivorum* xylose was one of the most available carbon compounds under all culture conditions. Arabinose and xylose were utilized by *Glomerella cingulata* (Hawkins, 1915) and by some species of *Pythium* (Saksena and Mehrotra, 1949). The results obtained in the present study show that the pentoses support fair growth of the species of *Phytophthora* under investigation.

Of the hexoses, dextrose served as the best source of carbon. Growth in galactose, laevulose and mannose was inconsistent. In most cases galactose supported fair amounts of growth, although it has been reported as a poor source of carbon for a number of fungi by different workers. Horr (1936) in case of *Aspergillus niger* and *Penicillium glaucum*, Kinsel (1937) in *Diplodia zea*, and Edgecombe (1938) (by linear growth measurement in Petri-dishes) in case of *Phytophthora cactorum*, *Saprolegnia ferax* and other fungi showed that galactose was a poor source of carbon. Bhargava (1945) found galactose to be useless for some members of the family Saprolegniaceae. On the other hand, Saksena and Mehrotra (1949) found some species of *Pythium* being able to utilize galactose. Mosher et al. (1936) and Ledeboer (1934) even found galactose to be a good source of carbon for *Trichophyton interdigitale* and *Ceratostomella ulmi*.

Cantino (1949, p. 102) reports that, "with reference to the hexose sugars, compounds with the same basic configuration around carbon-atoms number 3, 4, 5, and 6 as is found in glucose were suitable as carbon sources for growth. On the other hand, galactose and sorbose, which differ in this respect from glucose, mannose, and fructose, did not support growth." But the author found that in the fungi investigated by him this rule was not applicable because in the present study galactose also supported growth.

Of the disaccharides both maltose (which possesses a 1–4 linkage and is composed of glucose-*alpha*-glycoside unit) and sucrose (which is hydrolyzed by maltase and which contains a glucose unit that has the *alpha*-configuration) were readily metabolized. Similar observations have also been made by Cantino (1949) with *Blastocladia* and by Saksena and Mehrotra (1949) with *Pythium*. Bhargava (1945) found that maltose was a good source of carbon for the saprolegniaceous fungi investigated, but sucrose did not support growth except in *Brevilegnia gracilis*. Lactose, a glucose-*beta*-galactoside, supported fair growth. The same was the case with some species of *Pythium* (Saksena and Mehrotra, 1949) and *Brevilegnia gracilis* (Bhargava, 1945).

Raffinose proved to be a poor source of carbon for these fungi.

Of the polysaccharides, soluble starch was the best source of carbon for these fungi. Similar observation was also made with *Pythium* species investigated by Saksena and Mehrotra (1949).

Of the alcohols, glycerine was the best source of carbon for *Phytophthora* species. It has been reported to support growth of some species of *Pythium* (Saksena and Mehrotra, 1949 and Volkonsky, 1933) but it was found to have no effect on *Saprolegnia*, *Aphanomyces* (Volkonsky, 1933), and *Phymatotrichum omnivorum* (Ezekiel et al., 1934).

The glucoside amygdalin was of little use to the *Phytophthora* species investigated.

The pH determinations show that growth of fungi is always accompanied by acidification of the medium, but not definitely related to the amount of growth.

SUMMARY

The relative growth supporting values of several different carbohydrates, alcohols and the glucoside amygdalin were determined quantitatively in the case of a number of species of the genus *Phytoph-*

thora, viz., *P. cactorum* (Leb. et Cohn) Schroet., *P. citricola* Saw, *P. fagi* Hart, *P. meadii* McRae, *P. paeoniae* Cooper et Porter, *P. parasitica* Dastur, *P. parasitica* Dastur var. *nicotianae* Tucker, *P. parasitica* Dastur var. *piperina* Dastur, *P. pini* Leonian, *P. Richardiae* Buisman.

Maltose, sucrose, soluble starch, and dextrose were the best carbohydrates utilizable by these fungi. Of the alcohols, glycerine and sorbite were the best sources of carbon. Amygdalin was found to be of little use to these fungi.

Of the carbon compounds tested, maltose, sucrose, and soluble starch were the best sources of carbon. Dextrose, lactose, inulin, glycerine, and sorbite proved to be mediocre sources. Arabinose, rhamnose, xylose, galactose, laevulose, mannose, raffinose, dextrin, erythrite, mannite, dulcite and amygdalin were the poorest sources of carbon.

In each case the growth of the fungus was accompanied with acidification of the medium.

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